Damsels and distress: Factors affecting Haemulidae distribution on Bahamian reefs

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Abstract

The interconnected habitats of coral reefs, mangroves and seagrass are home to a quarter of all known species in the marine environment. The interconnectivity of these areas improves species richness and density, even for species that do not use the habitats as a nursery. The communities that live as part of these ecosystems, just like many other marine species, are vulnerable to the effects of anthropogenic noise. *Haemulidae spp.* use the patch reef system protected by the Cape of Eleuthera as an intermediate nursery and exhibit a complex relationship with *Stegastes spp.* The importance of coral reef flats, such as those of Eleuthera, remains a crucial knowledge gap in our understanding of the coral reef nursery ecosystem. Also lacking is an understanding of the effect of chronic boat traffic on entire coral reef fish communities. This thesis aims to address these knowledge gaps across three chapters. Chapter 1 provides a literature review exploring *Haemulidae spp*. in the tropical marine environment and the importance of nursery habitats; Stegastes species in the tropical marine environment; and, the effects of anthropogenic noise in the marine environment. This highlights the current knowledge gaps and guides the data chapters. Chapter 2 presents a study in the patch reef system identifying the settlement habits of three *Stegastes spp.* (*S. leucostictus, S. diencaeus, S. partitus*) and the relationship with local *Haemulidae spp.* populations. This study identifies that this interaction may be an indication of reef health, as well as shedding light on a competitive hierarchy that exists amongst *Stegastes spp*. Chapter 3 presents a community level study (53 species, 14,970 individuals, 6 patch reefs) comparing the reactions of the patch reefs either communities protected from or exposed to chronic boat traffic. The chronic effect of boat traffic had a detrimental effect on density, species richness and recruitment compared to similar reefs. This was particularly noticeable with the *Haemulidae spp.* using the patch reef system as an intermediate nursery. This could mean that chronic boat traffic is influencing recruitment as well as having wider implications for reef health.

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Definitions and abbreviations

Acoustic telemetry: Acoustic tags allow the tracking of movement.

Agonistic interactions: Aggressive behaviour, associated with fighting.

Alarm response: Reaction to a perceived threat.

Ambient noise: Natural soundscape consisting of biological (e.g. fish, invertebrates) and physical (e.g. rain, wind) sounds.

Anthropogenic noise: Anthropogenic threats are those produce by humans.

Artificial reef: Underwater structure built by humans to simulate a coral reef.

Auditory brainstem response: An auditory output taken from the electrical stimulus in the brain.

Auditory threshold: The minimum sound levels that can be detected at a specific frequency.

Barotrauma: Physical injury causes by changes in pressure.

Benthic substrate: The structures at the bottom of a body of water.

Big Bubble Curtain: The use of bubbles underwater to create insulation against anthropogenic noise.

Biophony: The production of sound, deliberate or incidental, by living organisms.

Biofouling: The fouling of structures, such as ships, by creatures such as barnacles.

Calcareous: Containing calcium. Hardens structures.

Carbon sink: Absorbs carbon dioxide.

Catadromous: Migrates down the river to spawn in the sea.

Cleaning station: Species are cleaned by smaller organism which remove dead skin and ectoparasites.

Cut: An inlet deliberately dug into land to form a protective shallow water dock.

Diurnal pattern: Daily repetition. Therefore, a diurnal chorus occurs daily.

Echolocation: The use of self-generated sound to locate object. May be used to navigate and find food.

Frequency: Recurrence of a wavelength in a certain period of time. Measured in cycles per second (Hertz, Hz).

Haemolymphatic bioindicator: A fluid found in body cavities and tissue that can be chemically analysed.

Haemolymphatic response: a change in the fluid as a reaction to an exterior influence.

Home range: An area occupied or frequently travelled in by an organism, may be part of a territory.

Hull slap: the noise emitted when waves impact on the hull of a boat.

Hydrophone: An underwater microphone that uses a piezoelectric transducer to convert local pressure changes into an electric signal that can be recorded.

Hydrophone array: Multiple hydrophones that used together can triangulate acoustic signals to locate a sound source.

Individual fitness: Sexual success; the contribution to the gene pool.

Locomotor activities: The physical activity that moves an individual.

Metamorphosis: A radical change in body plan during ontogeny.

Ocean acidification: The process of carbon dioxide absorbing into the ocean from the atmosphere, lowering pH.

Ocean energy systems: IEA agency focusing on harnessing the oceans energy to produce energy.

Otolith: Calcareous body used to sense sound and movement.

Passive acoustic monitoring / detection: Analysis using soundscape recordings.

Physiological damage/ stress: Damage to the body / an organism's response in reaction to an exterior stressor.

Pile driving: The process of driving large poles into the ground as seabed foundations.

Playback: The reproduction of recorded sounds using speakers.

Reef recruitment: The arrival of organisms at reef habitat, usually at the end of the pelagic early life phase.

Seismic air gun: Pneumatic gun using pressurised air used for conducting surveys of sub-seabed geology.

SONAR: SOund NAvigation and Ranging: Used by ships for navigation and detection.

Sound propagation: The movement of sound through a medium such as air or water.

Soundscape: The combination of sounds from an environment.

Special Area of Conservation: Similar to a Marine Protected Area, it is a location designed to protect the species within its bounds.

Stair case method: Also known as the method of adjustment. Stimulus is adjusted up when missed and down when noticed to identify an individual's threshold.

Startle response: instantaneous response to a stimulus perceived as a threat.

Temporary Threshold Shift: A change in an individual's ability to detect a stimulus, likely caused by excessive exposure to intense and/or prolonged sounds.

AIS: Automatic Identification System

CEI: Cape Eleuthera Institute

dB: decibels

DCS: Decompression Sickness

FL: Florida

GIS: Geographic Information System

GPS: Global Positioning System

Hz: Hertz

LFAS: Low Frequency Acoustic Signal

LNG: Liquid Natural Gas

MFAS: Medium Frequency Acoustic Signal

MPA: Marine Protected Area

ms: millisecond

ms^{-1}: metres per second

MSFD: European Commission Marine Strategy Framework Directive

NY: New York

SAC: Special Area of Conservation

SONAR: SOund RAnging and Navigation

µPa: micro Pascal

1. Introduction

1.1 Introduction

Eleuthera is located at the eastern edge of the Commonwealth of the Bahamas on the Great Bahama Bank (*Figure 1.1)*. The island forms a long thin border to the Atlantic Ocean to the East, with the northern and southern tips curving around to the west to form a protected body of water. The north of the island curves round into Harbour Island, which forms a gateway down the Bahama ridge that delves deeper into the Atlantic by Great Abaco. The west of the island drops offs into the Exuma Sound, which is buffered by a large area of sandbars and cays. The south of the island splits with a tip heading south towards Cat Island and the Cape of Eleuthera projecting to north-west towards the sandbars. This provides protection from heavy seas to a large body of shallow water. In the area protected by the Cape of Eleuthera there is a system of more than 200 patch reefs. These are likely interlinked with the small areas of seagrass found in the same area as well as the mangroves that spread from near the tip of the Cape around to Rock Sound. This mangrove system is an ideal habitat for many species as well as a nursery location for species that move onto the forereefs in the drop off into Exuma sound to the west. Most of the area has a calm tide with the exception of where the tide becomes trapped between the sandbars and the tip of the Cape, where a powerful tide exists. The power of the tide over time has a visible effect on the area, as the patch reefs in this area tend to be much smaller than in the rest of the system.

Eleuthera has human settlements spread throughout island, with many of these contributing to boat traffic. Prominent sources of boat traffic around the Cape of Eleuthera are the Cape Eleuthera Marina, the Cape Eleuthera Institute, local fisherman and the dock at Rock Sound.

Figure 1.1. Prominent features of the Cape of Eleuthera coral reef ecosystem. (1) Patch reef flats. (2) Mangroves. (3) Sandbars, cays and channels. (4) Fore reef drop off. The blue letters from left to right: Cape Eleuthera Marina (A), Cape Eleuthera Institute boathouse cut (B), Rock Sound dock (C).

1.2 Literature review

1.2.1 Haemulidae spp. niche in the tropical marine environment and the importance of nursery habitats.

Coral reef fish use a variety of strategies to improve their chances of survival. Many species utilise ontogenetic habitat partitioning with adults dominating coral reefs, which have the highest species richness, while juveniles form populations in mangroves and seagrass beds (Jaxion-Harm et al., 2012). Active attraction or avoidance of these habitats can be guided by a variety of sensory cues including olfactory and acoustic signals (Simpson et al., 2008; Huijibers et al., 2012). Variable habitat combined with reaction to sensory cues enables ontogenetic shifts for life stage partitioning, which depends upon the interconnectivity of the ecosystem. The Cape of Eleuthera (N 24°50'05", W 76°20'32"), The Bahamas, is a prime example of how a consecutive chain of habitats consisting of seagrass, mangroves and patch reefs, can be an ideal nursery habitat for juvenile fish before they move out on to forereefs. The waters inside the Cape are protected from the Atlantic Ocean by a large area of sandbars, which may also act as a further staging point before fish transition out to larger reefs. Surrounding the water is a multitude of tidal creeks in which mangroves have developed. There are a limited number of seagrass patches, and a system in excess of 200 patch reefs (*Figure 1.1*). All the habitats that make up this interconnected ecosystem each play their own unique role (Harborne et al., 2013). The mangroves and sea grass beds frequently perform as the most successful nursery habitats, able to replenish surrounding reefs, including those geographically separated from adjacent nursery habitat (Huijbers et al., 2013).

Interconnectivity of these habitats is beneficial to ecosystem health. Reefs tend to have the highest number of species and individuals ahead of mangroves, while seagrass beds tend to have the lowest values for both these variables (Honda et al., 2013). 14% of the species

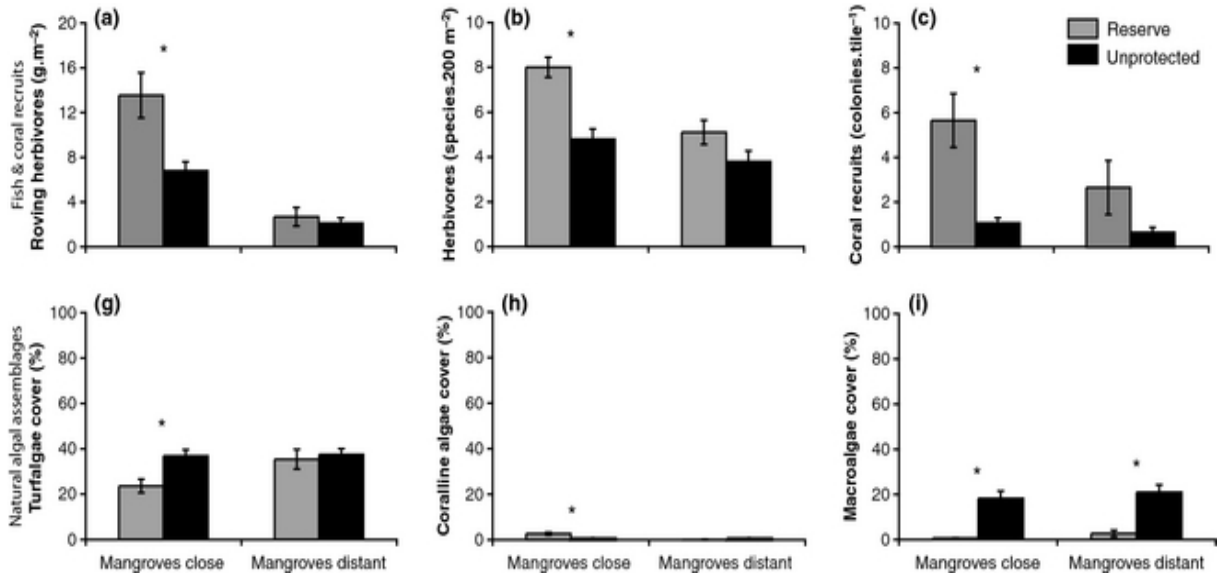

Figure 1.2. Effects of reserves and connectivity on: roving herbivore biomass (a); density of coral recruits (c); cover of turf algae (g). Figure from Olds et al., 2012. Graphs d-f, representing tile turf algal cover, are not presented as these outputs are only relevant in the context of the original study.

surveyed in this study were found in more than one habitat, some of which will have been due to ontogenetic habitat changes. The connectivity between sites can replenish multiple coastal habitats, which indirectly influences settlement of other species that do not rely on the nurseries to settle at these sites as well (Kimirei et al., 2013). The effectiveness of these interconnected nursery grounds is such that they are more influential in maintaining the population of smaller bodied fish than protection from fishing (Nagelkerken et al., 2012). Fishery protection is more effective for large bodied species, including many herbivores that are regularly harvested. Protection of herbivores is important as these species exhibit a symbiotic relationship with coral that improves reef health. Grazing on macroalgae by herbivores improves coral cover as well as recruitment, a relationship that is enhanced by a reef's interconnectivity with mangroves (Yabsley et al., 2016). With the correct design of Marine Protected Areas (MPAs), fishing could continue in certain areas without dilapidating the beneficial effect that large bodied herbivores bring to an ecosystem. The combination of

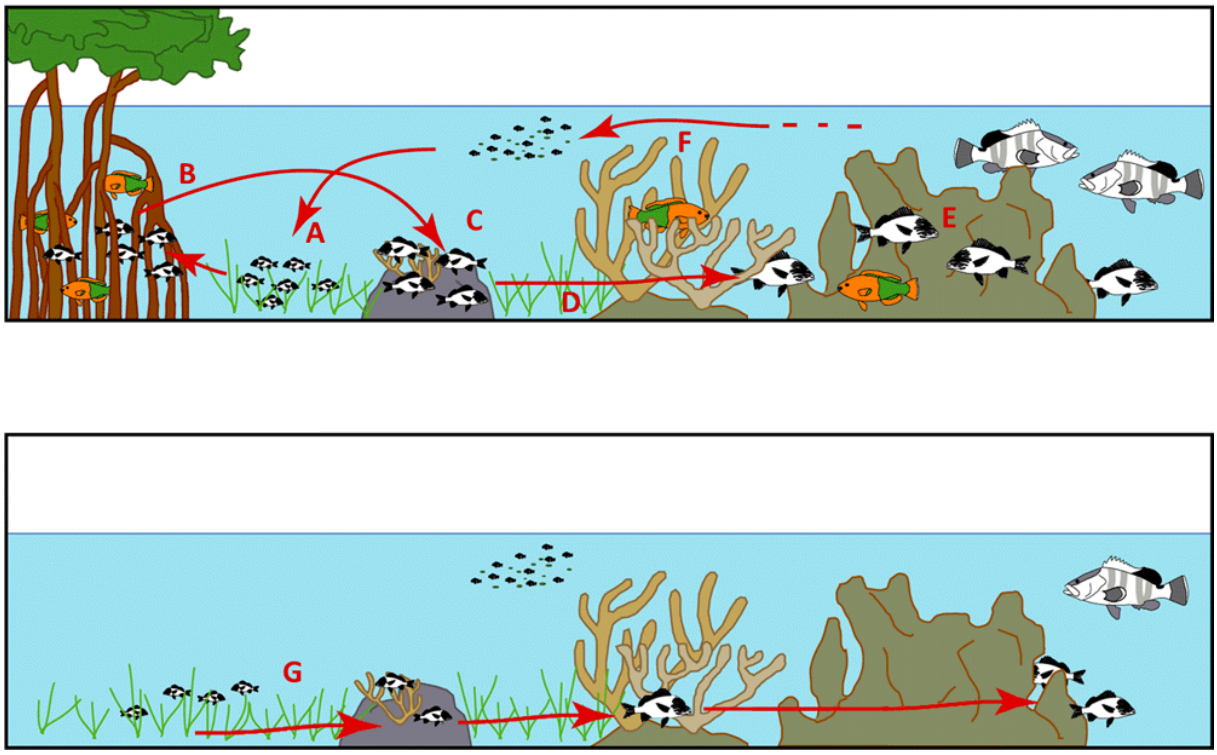

Figure 1.3. The effect of an interconnected habitat on reef population. Larvae return from pelagic life phase (F) and use the cover of the sea grass to grow (A). As they develop, they move into the mangroves (B) for better protection followed by the patch reef system (C) that acts as an intermediate stage before progressing onto larger reefs (D) and finally moving onto a forereef (E). The lower image represents the transition of habitat without mangroves (G); juvenile fish transition from seagrass onto patch reefs, followed by shallow forereefs (2-5m depth), and finally onto fore reefs (9-12m depth). Taken from Mumby et al., 2004.

an interconnected system with a marine reserve improves herbivore populations (Olds et al., 2012) (*Figure 1.2*).

Many species rely, or partially rely, on mangroves and seagrass as nursery habitats for their juvenile life stage. Areas lacking in, or without, these habitats have reduced populations of the species on surrounding coral reefs (Nagelkerken et al., 2001; Nagelkerken et al., 2002; Nagelkerken & van der Velde, 2002). Although it is possible for juvenile fish species to occupy other habitats, mangroves provide an intermediate stage nursery that improves survival of the species that utilize them (Mumby et al., 2004) (*Figure 1.3)*. The beneficial effect of nursery

habitats can reach wider than the immediate reefs and may support surrounding habitats, up to a regional scale. 8 of 12 species studied that use mangroves as a nursery were found to have their population on surrounding reefs limited by the availability of mangroves (Serafy et al., 2015). Many individuals leave mangroves as they progress into an adult life stage and move onto coral reefs, where the influence of a successful mangrove on the total population is strong. Destruction of mangroves supporting a reef can significantly dilapidate fish stocks (Mumby et al., 2004). Usage of nursery habitats appears to vary geographically. The use of mangroves as a nursery being more prolific amongst species in the Caribbean than the Indo Pacific, with *Haemulidae spp.* being noted as one of the key users (Igulu et al., 2014). Although mangroves are used less by species in the Indo Pacific, 85% of those that do use the habitat as a nursery for their juvenile life stage stayed in the same mangrove until moving onto a nearby reef (Paillon et al., 2014).

Each species has their own niche and will use nursery habitats differently (Wilson et al., 2010). Mangroves and seagrass beds have been shown to be of particular importance to juvenile French grunt and blue striped grunt (*Haemulon flavolineatum and H. sciurus*) (Nagelkerken & van der Velde, 2004a, 2004b). Olfactory cues guide species to mangroves and seagrass beds while acoustic cues are important for recruitment to coral reefs (Huijbers et al., 2012). As *Haemulidae spp.* grow, they move deeper and become more vulnerable to predators, which may influence when, alongside the reaction to the various habitat cues, individuals of these species move from mangroves to reefs (Grol et al., 2011; Jordan, 2012;). Moving at the right size is imperative for survival. Juvenile *H. flavolineatum* had 0% survival rates on reefs, but up to 47% in non-reef habitats. Contrastingly, adult *H. flavolineatum* showed between 77-100% survival rates, with larger adults having increased chances of survival on reefs as they grew (Grol et al., 2011). The mangroves are primarily used for shelter due to the physical structure they provide, however *H. flavolineatum* will break from this cover in order to forage amongst the sea grass (Vaslet et al., 2015). Juvenile *Haemulidae spp.* continue nocturnal foraging even amongst an invasive species of seagrass, which suggests that the physical

protective shelter for hunting provided by seagrass is more important than the species (Olinger et al., 2017). Once living on a reef, foraging becomes a solo activity. The few juvenile *Haemulidae spp.* remaining will seek nourishment in the water column, while adult *Haemulidae spp.* forage around rocky and sandy areas. After finishing foraging, the species then schools near the bottom of reefs for protection, lowering their swimming speed (Pereira & Ferreira, 2013). Schooling like this, coupled with increased population density, offers *H. plumieri* individuals health and survival benefits (Yeager et al., 2014).

There are a range of anthropogenic threats facing all aquatic systems that are a concern to biodiversity and ecosystem processes (Crook et al., 2015), many of which will affect marine communities. For many of the habitats that are occupied by these communities, a wide knowledge gap still exists, especially for coral reef flats which may be being used by species as nursery (Harborne, 2013). Given the lack of research on coral reef flats and the importance of auditory cues for habitat selection for *Haemulidae spp*. (Huijbers et al., 2012), the studies in this thesis will aim to address some of the knowledge gaps on communities of reef flats as well as exploring effect of anthropogenic noise on these communities. The reef flats in the Cape of Eleuthera provide an ideal study location, exhibiting the important interconnectivity with the surrounding mangroves and larger reefs (Figure 1.1), as well as hosting a population of *Haemulidae spp.*

1.2.2 *Stegastes* species in the tropical marine environment

Stegastes spp. are a vital part of many coral reef communities. Damselfish are herbivores (Ceccarelli et al., 2001), often referred to as a gardener species. The species appears to excel in abundance and biomass even where other herbivores, especially grazers, do not. The genus has been able to take advantage of their small individual biomass and have found a niche where increasing anthropogenic influences appear to aid them by deterring competitors. In areas that are not protected fisheries or have no fishing restrictions, *Pomacentridae* showed

an increase in biomass and abundance, opposing the outcome of the larger bodied consumers of the algal communities on a reef (Edwards et al., 2013). The family occupies most reefs but were found to have higher biomass on fringing reefs in Madagascar than on patch or barrier reefs (Harding et al., 2006). Behaviours commonly exhibited by the genus include gardening algae, killing corals, and chasing away species invading their territory. This makes them particularly important in structuring the algal reef community. (Potts, 1977; Mahoney, 1981; Ferreira et al.,1998; Hata et al., 2002; Hata & Kato 2003). Their algal grooming maintains a high algal biomass when compared to areas without Stegastes spp. (Hixon & Brostoff, 1981; Klumpp et al., 1987; Hixon & Brostoff 1996;). An investigation into algal communities within *Stegastes spp.* territories in the Indo-Pacific determined that they influence nutrient enrichment and are able to exclude other herbivorous species. These territories had a higher level of algal biodiversity, with an increased coverage of brown macro algae in particular. Outside of the territories there was an increase in percentage cover, as well as the biomass of red macro algae but less overall diversity of algal species. The exclusion of herbivores alongside nutrient treatment, enhanced algal growth rates, suggesting that *Stegastes spp*. are important for maintaining algal beds (Gobler et al., 2006). A study in Japan found that dusky farmerfish (*Stegastes nigricans*) farms were dominated by a filamentous rhodophyte, *Womersleyella setacea*, with territories having an increased species richness and biomass. Conversely to other studies, outside of the territories it was recorded that there was higher species diversity and evenness. *W. setacea* was the dominant species throughout the year long sampling period, which correlates with the findings of other studies as to the construction of algae within damselfish habitats globally. However, the one species dominance and low diversity found here is a contrast to previous studies where interruption of grazing, due to *Stegastes spp.* aggressively removing intruders, enhanced algal species diversity. This appears to be due to *W. setacea* trapping sediment, making it difficult for other algal species to settle, alongside that *S. nigricans* choice to weed indigestible calcareous and thicker algae whereas other *Stegastes spp.* may be less selective with their algal gardening. This study was supplemented by the placement of artificial slate plates inside and outside of damselfish

territories. Within a *S. nigricans* territory, *W. setacea* gained biomass achieving a level of biomass akin to that on the natural substrata. Outside, undisturbed grazing of the plates by herbivores allowed succession by early colonizers of various morphologies. As with the study of algal communities on natural substrata, the combination of sediment trapped by *W. setacea* turf alongside the selective weeding by *S. nigricans* excluded other algae and removed competition leading to low species diversity whilst maintaining a high biomass (Hata et al., 2002). Diet of *Stegastes spp*. is not restricted to algae, and this has led the species to be considered as a keystone for structuring benthic communities on coral reefs. Stomach contents of two species of damselfish, Brazilian damselfish and cocoa damselfish (*Stegastes fuscus* and *Stegastes variabilis*), found on algal dominated costal reefs were analysed with 80% of algae found in stomach contents was calcareous algae, which is thought to be representative of the algal community within their territories. This high percentage of calcareous algae had a positive linear relationship with non-calcareous algae as the former provides a base for the latter to grow on. The total algal matter found in *Stegastes spp.* stomach contents is more than 70% with another ~15% consisting of invertebrates and detritus. Diatoms followed by filamentous algae were most common in diets of juveniles and adults of both species, which also showed positive food selection for all but the calcareous algae. The importance of this data is that the garden maintenance keeps, in the most part, algae that has evolved to be herbivore deterrent whilst being a host for the other sources of damselfish diet (Feitosa et al., 2012). The effect of dusky damselfish, *Stegastes adustus*, in benthic communities living amongst rocky shores in the southeast Atlantic (Brazil) keep algal communities in the early succession stage, stopping them from becoming dominated by *Jania spp*. Biodiversity and biomass of epilithic algae and cryptofauna communities are distinctively higher within territories. The diet of *S. adustus* is 70% algae, 30% animal matter. Grazing rate did not change considerably between seasons but could wipe out primary production during winter (Ferreira et al., 1998). The gardening behaviour is known to influence coral populations in Kenya. The jewel damselfish, *Plectroglyphidodon lacrymatus*, that defended a territory and protected its algae garden had a detrimental effect on juvenile corals (Gordon et al., 2015).

It is more than just the algal and coral communities that can be influenced by *Stegastes spp*. Longfin damselfish (*Stegastes diencaeus*) were placed in artificial shelters within slippery dick (*Halichoeres bivittatus*) home ranges. The arrival of a *S. diencaeus* did not reduce the size of territory that *H. bivittatus* travelled but did change the locations of the wrasses' home range. This led to the conclusion that aggressive *Stegastes spp.* affect the space use of individual wrasse, which may in turn effect the spatial use of the wrasse population (Jones, 2005). Another egg predator, blue-headed wrasse (*Thalassoma bifasciatum*), was used to test the aggressive behaviour of egg guarding and non-egg guarding male beaugregory damselfish (*Stegastes leucostictus*). There was no change in amount of high risk aggressive behaviour for single or multiple wrasse presentations, but low cost interactions did increase. There was a notable change for egg guarding males who were more likely to engage in aggressive chases (Haley & Müller, 2002). The presence of egg predators and *Stegastes spp.* is clearly mutually influential, but if a damselfish is settling in an area heavy with egg predators it must compromise defence of its nest against algal grooming, courtship and visits to cleaning sites. The value of using a cleaning station for a longfin damselfish (*Stegastes diencaeus*), like other species, requires a cost benefit analysis by any individual making the journey. As travel time and distance increased, so does the number of attacks by other territorial fish. This becomes an increasingly costly act as more time away also leads to more intrusions by grazers on the travelling damselfish's territory. There will be a decrease in parasitic gnathiid isopod larvae for any *S. diencaeus* that live closer to the cleaning sites, however, it is noted that the species are willing to travel further and spend more time away for social and reproductive acts (Cheney & Cote, 2001). Cleaning stations within *Stegastes spp.* territories are visited much more infrequently than those outside of territories, with the most frequent visitor being the owner of a territory. Gobies (*Gobiidae*) reduced the time and rate of cleaning of clients due to persistent attacks from *Stegastes spp*. Although intrusion rates for territories with and without cleaning stations were similar, damselfish with a cleaning station chased off intruders more regularly than those without a cleaning station leaving them open to the negative consequences of a decreased foraging rate as well as an increase in egg predation due to an increased freedom

of movement of visitors to the territory. The positive value of the cleaning stations versus the negative consequences is undetermined. *Stegastes spp*. have a significant effect on cleaning stations, and suffer as much themselves, which raises questions as to the reasons for them to settle near one another (Arnal & Cote, 1998). From these examples, the support for *Stegastes spp*. to be considered a keystone species is high due to the influence the species has over other fish species, control of algal population and limitations it may impose onto coral. Choice of where a damselfish settles will have a noticeable effect on the community around them, but this is somewhat a two way interaction with damselfish preferring to settle with and without certain other species.

Even intra-genus interactions will influence settlement. Selection of an appropriate territory to settle in relative to other *Stegastes spp.* could have a vast effect on life duration and reproductive success. For larger males returning to settle, finding a territory away from another male will significantly reduce chances of mortality. Conversely, it is advantageous for a smaller male who is less likely to suffer from attacks from small fish and egg predators when near to another larger male, but does not have the increased levels of mortality that larger settling males will suffer (McCormick & Meekan, 2007). There are other identifiable factors effecting courtship that may influence a *Stegastes spp.* territory selection. Courtship success was measured as the number of egg batches collected per week with variables showing a significant correlation in; frequency of courtship, inter- and intraspecific aggression, total length of courtship and male territory size. Female selection of mates appears to be the dominant form of sexual success, but a poorly selected territory may lead to courtship success being influenced by the other variables (Schmale, 1981). Attempts at reproductive success could come at more of a cost than having the ideal territory for those native to the Caribbean. The eruption of Lionfish (*Pterois volitans* and *Pterois miles*) populations provides a new threat that beaugregory damselfish (*Stegastes leucostictus*) may recognize as a predator but will not interrupt high risk courtship acts to avoid (Black et al., 2014). This may mean that damselfish will not select predator avoidance over a territory that may increase courtship success. Varying

the densities of *Stegastes spp.* on reefs can change their behaviour with an increased presence of the genus reducing territorial behaviour and leading to a dominance hierarchy. This hierarchy causes a different rate of growth amongst the *Stegastes spp*. present, with a coinciding decrease in average density of the whole community as the density of damsels increased. Yellow tailed anthias (*Pseudanthias flavicauda*) departed from the reefs faster than *Pseudanthias wardi*. There was not a link shown with mortality through lack of food, and there did not appear to be a link to over competition either even up to 50 times the normal density of damselfish (Doherty, 1982).

A similar study to a following chapter of this article was conducted in another area of the Caribbean, this time with a focus on areas of larger reefs. *Stegastes spp.* were found to be more abundant on larger, more complex colonies of *Monstrea spp*., which had numerous holes that were large enough for *Stegastes spp*. to pass through. The relationship between *Stegastes spp.* and mean coral height was significant to the extent that the latter was able to predict the abundance of the former (Harborne et al., 2011). *S. diencaeus* were characterized to quantify variables that determined factors that are important in adult settlement. Experimental removal was carried out to determine recolonialization times. The presence of a nest led to the fastest re settlement, whereas substrate, rugosity and presence of cleaning stations appeared to have little or no effect. Males returned to sites fastest, and would be most likely to settle on sites, that had been previously used as nest sites. This suggests that intraspecific competition for high-quality nest sites may generate sex differences in territory relocation and highly stable sex-specific patterns of adult distribution (Cheney & Cote, 2003). Three spot damsels (*Stegastes planifrons*) positively correlate with the size of Staghorn coral (*Acropora cervicornis*), however on larger patches there was a negative correlation indicating contiguous territorial borders. Males would competitively exclude juveniles *Stegastes* and *S. adustus* from territories; whilst females select boulder star corals instead. Breeding occurs on a year round lunar cycle where females would lay clutches of eggs in male territories. *S. planifrons* were experimentally removed and were replaced within 48 hours in a hierarchy as

follows: (1) non-breeding pool of wanderers, (2) resident damsels abandoning their own territories, (3) replacements by *S. adustus* and immature *S. planifrons*. Reduced aggression replaced by intra-species cooperation by *S. planifrons* living on large coral patches gave an increased persistence of stability to the population with any adjustment to the stable population being from the pool of wanderers (Williams, 1978).

Many of the interactions during the earlier mentioned studies will have involved vocal communications between *Stegastes spp.*, making auditory threshold an important consideration when studying the genus and the wider family. Sergeant major damselfish (*Abudefduf saxatilis*) were used in an early study of responses to acoustics cues. Fish from a size range of 11–121 mm were exposed to a variety of acoustic cues and monitored using the auditory brainstem response technique. At lower frequencies (90–380 Hz), thresholds increased with increasing body size, with all fish being most sensitive to this range. *A. saxatilis* have poor hearing sensitivity compared to most generalists, including other damselfish, and it is therefore likely they only use acoustic cues for local-scale orientation (<1 km) (Egner & Mann, 2005). This poor hearing may be due to co-evolution with methods of intra-species communication, with sounds being produced when within 1–2 body lengths of the intended receiver at a level and frequency akin to the audible range (90–380 Hz, 123–127 dB re 1 μPa) (Maruska et al., 2007). The poor hearing has not limited *Stegastes spp.* from interpreting what they do pick up, with *S. partitus* demonstrating the hearing sensitivity to discriminate between the structurally similar tri-chirp courtship sounds produced by conspecifics and the sympatric species *S. leucostictus and S. planifrons* (Myberg & Spire, 1972). Not only able to discriminate between individual sounds, but *Stegastes spp.* are part of the family of fish (*Pomacentridae*) captured in largest numbers in light traps playing reef noise when settling following a pelagic life phase, suggesting that sound is an important navigational tool (Simpson et al., 2004).

Stegastes spp. are highly abundant in coral reef communities, making up half of fish biomass in many communities (Ackerman & Bellwood 2000). The importance of sound in the

recruitment of the genus and their effect on other species in the community makes them a valuable focal group of species for relatively understudied coral reef flats.

1.2.3 Anthropogenic noise in the marine environment

The global marine environment is changing, forcing marine organisms to environmental change or shift in biogeographical range to new ecosystems (Simpson et al., 2011a). Humans are intrinsically linked to many of these changes. Energy production fuelled by coal, oil and gas contributes vast volumes carbon dioxide (CO_2), amongst other gases, into the atmosphere. The data in the Paris Accord states that the 43 Annex I nations alone contributed 13,572,019.97 kt of CO_2 into the atmosphere in 2015 (United Nations Framework Convention on Climate Change, 2015). Through the Greenhouse Effect, this causes warming of the oceans which is melting the ice caps, but it also causes ocean acidification due to the ocean acting as a carbon sink (Le Quéré et al., 2009). Moreover, humans are having more direct effects on the oceans. Overfishing has a visible effect and is easily quantifiable by monitoring fish stocks, however anthropogenic noise is having a detrimental effect that may be less obvious. Offshore pile driving, boat traffic, seismic surveys using air guns and SONAR are just a selection of contributions made by humans that impact the marine soundscape. Three of these noise sources include sounds in the very low frequency range (<100 Hz), overlapping and masking communication between whales (~20 Hz) (Wilcock et al., 2014) (*Table 1.1; Figure 1.4*). This has a direct impact on whales, masking their echolocation, causing rapid ascents and leading to mass strandings (Cox et al., 2006; Tyack et al., 2011). Anthropogenic noise is now recognized as being a significant issue to the extent that the European Union Marine Strategy Framework Directive (MSFD) requires member states to monitor and reduce marine noise pollution. This review will address the issues associated with sources of anthropogenic noise and explore known effects on marine wildlife, before considering possible methods for protecting the natural marine soundscape.

Table 1.1 Contributors to the marine soundscape. The sources for whale vocalisations were recorded by Nieukirk et al., 2004; and Sirovic et al., 2007. Fewtrell & McCauley, 2012, was the source for seismic air gun. Invertebrate shells rubbing against benthic substrate by Freeman et al., 2014. Frequency of fish vocalisations and feeding activities recorded in study by Tricas & Boyle, 2014, while the sound range was published by Erisman & Rowell, 2017. Oil platform noise data from Gales, 1982. Aquaculture data from Davidson et al., 2009. Wind farm incidental anthropogenic noise data from Bergström et al., 2014*. Dredging recordings taken by Jones & Marten, 2016. Supporting data for frequencies from Slabbekoorn et al., 2010.*

Source	Frequency / kHz	Decibels / dB re 1µPa	Time
Blue Whale (*Balaenoptera musculus*)	18–29	189±3	25s
Fin whales (*Balaenoptera physalus*)	15–28	189±4	2 short pulses, 18 s apart
Minke whales (*Balaenoptera acutorostrata*)	30	-	Series of pulses 1 s apart
Fish	0–1.3 & 3.0–8.86	≤190	Deliberate vocalisations and incidental sounds.
Crustaceans	11–17	62–76	Incidental sounds from rubbing shell against substrate.
Shipping & Boat traffic	0.1–10	119–188	Inclusive of small vessels to large tankers.
Pile driving	-	166–218	-
Seismic air cannon	-	120–255	-
SONAR	0.1–180	131–224	-
Aquaculture	-	117–149	-
Dredging	0.02–1	160–180	-
Oil platforms	0.1–10	130–180	-
Wind farms	-	80–150	Vibration from gear mechanisms vibrating.

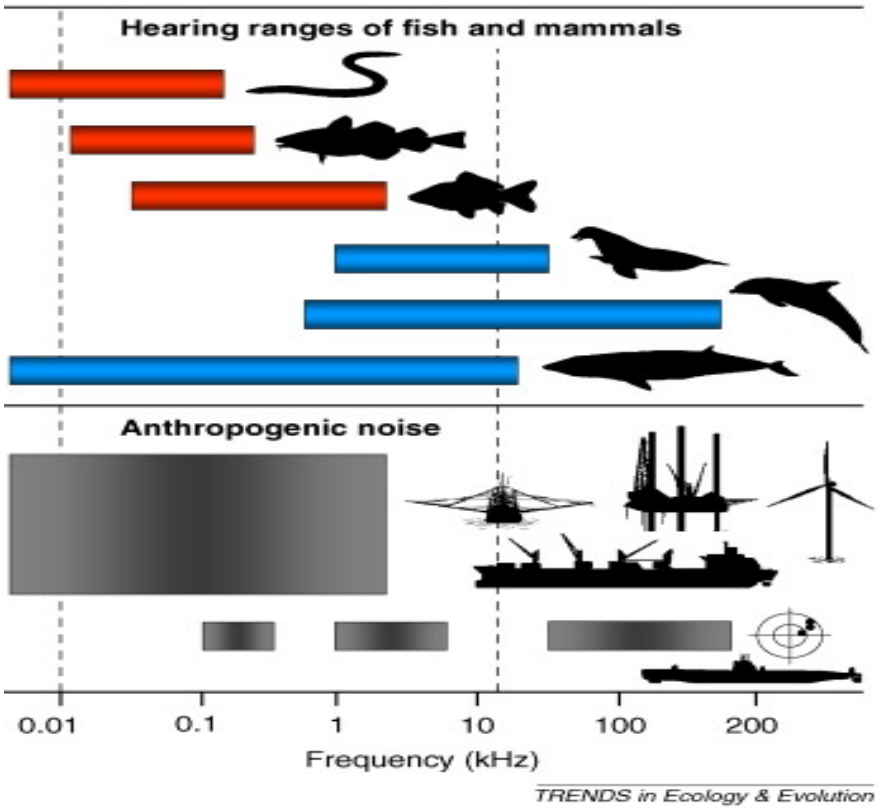

Figure 1.4. Frequencies within the hearing ranges of marine organisms alongside the frequencies of sources of anthropogenic noise. Taken from Slabbekoorn et al., 2010.

1.2.3.1 Pile driving

Pile driving is the use of machinery to drive heavy piles, large metal or wooden poles, into the ground to act as the foundation for a structure; a technique commonly used in the marine and coastal construction industry. As coastal development increases and the number of offshore sites used for the production of renewable energy grows, there is a rise in disturbance to marine creatures. At the site of construction for a liquid natural gas terminal in Latvia, a recording at 1 m from the pile reached 218 dB re 1 µPa and only fell to 190 dB re 1 µPa at 190 m from the source (Bagocius, 2015). This substantial noise level may affect the salmon migrating through the small straight as the sound level at the source is 122 dB above the salmon's hearing threshold, which is likely to cause hearing damage (Nedwell et al., 2007). Just as important as migrating routes, are marine protected areas (MPA). Often created mostly to reduce the threat to fisheries and protect vital ecosystems, the dangers posed by anthropogenic noise aren't always a consideration. 25 km from the Firth of Moray Special Area

of Conservation (SAC), pile driving for the installation of two wind turbines produced impacts of up to 205 dB re 1 µPA (at 100 m), but were still detectable at 80 km, well inside the SAC. This is of particular importance when it was noted that the local populations of bottlenose dolphins (*Tursiops truncatus*) showed alterations in behaviour up to 50 km away, and if within 100 m of the impact would have suffered auditory damage (Bailey et al., 2010). Snapping shrimp increased the number and amplitudes of snaps produced under playback of pile driving noise (Spiga, 2016). This suggests that snapping shrimp attempt to compete with the sound coming from the construction, or else that they react to auditory damage with increased sound production. Further damage could also occur as noise from reef invertebrates can be a driver for recruitment of larval fish and invertebrates, so masking of the natural soundscape with construction noise could diminish recruitment (Simpson et al., 2004, 2008; Stanley et al., 2011). Unconditioned crustaceans exposed to varying frequencies and amplitudes of substrate borne vibrations using the stair case method of presentation exhibited sudden bursts of movement as well as rapid bouts of movement in relation to the strength of stimuli (Roberts & Breithaupt, 2016). Given that rapid movements as a reaction to a stimulus have been associated with predator evasion in other marine organisms (Daniel & Meyhöfer, 1989), this highly exertive reaction could be a costly and unnecessary use of energy reserves.

Fish also experience stress in response to anthropogenic noise. Naïve fish respond with heightened ventilation, but after 12 weeks, they begin to adapt to the noise (Nedelec et al., 2016). Although the reduction of stress by adjusting to the exposure to the sound is a benefit as it suggests organisms could survive long term exposure without excessive physiological stress, it could be that this leads to the negative behavioural associations with anthropogenic noise such as interference of predator–prey interactions (Voellmy et al., 2014a; Kern & Radford, 2016). This theory is further supported by the reduction in startle response of European sea bass (*Dicentrarchus labrax*) following acute exposure using playback of anthropogenic noise (Everley et al., 2016). Aside from the negative effects on hearing, behaviour and physiological stress, there is a line of research that suggests there is no

physical harm caused by pile driving. Physiological damage by barotrauma injuries, damage from pressure related change within a body, did not occur in six fish species tested until 20 dB re 1 µPa above the interim noise produced from this construction technique (Casper et al., 2016). Before, during and after construction of a new wharf complex in Port Canaveral FL (USA), 15 Sheepshead and 10 Grey Snapper were monitored for behavioural changes using acoustic telemetry. From this, the study was able to deduce that there was no change to suggest any injuries or mortality. It was noted that there was a significant reduction in the population of mangrove snapper, but this could be due to natural movements of the species in the study area (Iafrate, 2016). Looking at previous evidence presented here, there is a prevalence of effects related to the exhibition of physiological stress or behavioural changes, not physical injury or death. This study could be furthered by a focus on behavioural changes as well as attempting to identify whether the disappearance of mangrove snapper occurred due to a natural movement pattern or not.

An alternate target of study has been to assess ability to reduce noise impact from construction, rather than just identifying the damage it may cause. In the Europe, the United States and Asia, research-led environmental planning has been conducted to reduce the effects of pile driving as a noise source at projects such as: pre-construction noise analysis and modelling for a new bridge in New York (USA); the use of a simple bubble curtain in Hong Kong, and mitigation monitoring during wind farm construction around the North Sea (Popper et al., 2016a; Verfuss et al., 2016; Wursig et al., 2000). One example of technology to reduce noise output was the use of the big bubble curtain during the construction of the Borkum West II wind farm in the North Sea. Noise reduction curtailed porpoise disturbance to approximately 90% (Nehls et al., 2016). In Hong Kong, a simple bubble curtain using a rubber hose was used, and even this reduced sound levels by 3–5 dB re 1 µPa. There was a reduced density of Indo-Pacific humpbacked dolphins (*Sousa chinensis*) following the construction demonstrating that the construction still had a negative effect on the population, but there were no overt changes to behaviour except for some small changes in swimming speed (Wursig et

al., 2000). Even with further research and planning, alongside demonstrations of the damage anthropogenic noise can cause and the positive impact of noise mitigation, there is still evidence that future construction may fall short of protecting marine mammals from injury. This is in part due to the cost versus benefit of noise reduction, or noise mitigation, is not fully understood (Dolman et al., 2016). Prior to the construction of the new NY bridge to replace the Tappen Zee bridge, construction techniques were scrutineered pending the issue of a construction permit. During construction, the environmental impacts were monitored. Notably, follow up research focused on the behaviour and movement of Hudson River Sturgeon around the Tappen Zee bridge construction. It is noted that the sturgeon stayed away from the area during pile driving and avoided exposure to pile driving noise above 187 dB re 1 µPa, far short of the 206 dB re 1 µPa pressure limit that is deemed to cause physiological damage (Krebs et al., 2016a, 2016b). However, by driving fish out of their habitat and forcing behavioural change, excessive noise production was clearly disturbing the fish present and may have exposed these organisms to excessive stress. Given that the study focused on just one species in the vicinity, and behavioural change was recorded, the question should be raised on how the rest of the community were affected, especially those that are less mobile. Similar sound levels to those produced in the new NY bridge construction were found to displace harbour seals (*Phoca vitulina*) during pile driving off the south-east coast of the United Kingdom. Up to 83% of seals in a 25 km radius left the area during piling when noise was between 166–178 dB re 1 µPa (Russell et al., 2016). Within two hours, however, the local population distribution returned to normal. This avoidance behaviour displayed by the harbour seal population may reduce the direct acute effects of pile driving but could also interfere with feeding behaviours by forcing the seals to abandon traditional foraging grounds.

Pioneering improved techniques is important for coastal and marine construction, so that rather than the wind farms being detrimental, they may ultimately become beneficial. Marine species can use the physical structures created in coastal developments as new habitats since

they become artificial reefs (Scheidat et al., 2011). Further, the new habitat becomes new foraging grounds for harbour seals (Russel et al., 2014).

1.2.3.2 Seismic air guns

Seismic air guns are used to survey beneath the seabed for potential oil and gas reserves. The noise produced by air guns varies on their size. Immediate responses to air gun noise can cause fish to cluster more, swim faster, move within the water column, as well as increase alarm response (Fewtrell & McCauley, 2012). A small gun (10,160 cm^3) used by Popper et al., (2016b), produced 231 dB re 1 µPa at 1 m; substantially more than the levels found in the pile driving studies. Paddlefish and Pallid sturgeon (*Polydontidae & Scaphirhynchus albus*) were treated with a single exposure from 1–3 m and at greater intervals, then monitored for seven days. During the study, there was no significant difference in mortality for control fish or those treated, neither was there any apparent injuries to those treated. This was only a single exposure while during real seismic surveys fish would be exposed to multiple firings at a varied distance, which should be considered when reviewing these findings. Equally, it would be difficult to determine how much stress was suffered by test fish due to the movement of fish between lake and tank in the wet laboratory, as there was not a period to allow for acclimatization, so even the move could have exposed subjects to varying extra levels of stress, making the condition of the control individuals nearer to those exposed to the air gun. It would also be easy to miss abnormal behaviour in fish as they were only monitored once every 12 hours. Unusually, some fish mortality is attributed to pile driving in the vicinity, whereas papers referenced previously in this review determine that the noise levels produced from pile driving activity is below the levels required for a barotrauma, yet the air guns used here far surpass it. The study notes the lack of difference in exposed and control fish, but this seems unsurprising given that the control fish were only 160 m away from the exposure and the sound produced by these guns is designed to travel long distances, penetrating the ocean floor. This concern is furthered by evidence that an air gun remains an impulse noise for up to 1000 km from source before attenuation causes it to become continuous noise. Seismic noise

is known to effect whales up to 2000 km away (Wittekind et al., 2016) and is detectable by hydrophones up to 3000 km away (Nieukirk et al., 2004). Our general understanding of the effects of seismic air guns falls short, as shown by controls implemented by the state of Alaska, USA. A study found that the modelled air gun effects submitted prior to use between 2006 and 2012 rarely showed any similarity to the actual outputs (Aerts & Streever, 2016). Not all control measures are so unsuccessful. In waters north of Russia, measures were put in place to limit the effects of seismic surveys on the grey whale (*Eschrichtius robustus*) population that feeds in the area during summer. The use of boundary areas, and observers combined with a smaller number and size of air guns meant that very few whales demonstrated signs of stress or appeared to leave the area (Johnson et al., 2007; Yazvenko et al., 2007). Further to this, it was noted in the years following the population has been growing by 3% annually (Cooke et al., 2007) and has grown by 20% between 2001 when the survey was first carried out and 2006 (Weller et al., 2002; Cooke et al., 2006). There is more evidence to suggest that there may be less cause for concern with this versus other sources of anthropogenic noise. Larvae of egg-bearing female spiny lobsters (*Jasus edwardsii*) were exposed to three air guns signals of more than 185 dB re 1 µPa at 1 m. The females were kept until their eggs hatched. After being caught, an acclimatization period was given prior to exposure to anthropogenic noise. The multiple exposures present a more realistic environment to the previous single exposure study with paddlefish, but showed that the larvae were unaffected (Day et al., 2016). A study of freshwater fish in Canada (adult northern pike (*Esox lucius*) and lake chub (*Couesius plumbeus*), once again found there was no physical damage to fish after exposure to air guns producing 175–180 dB re 1 µPa at 1 m (Song et al., 2008). This study noted a change in hearing threshold following the events, which could make the species more vulnerable to predation following exposure. A temporary shift in threshold was also detected in harbour porpoise (*Phocoena phocoena*) at 174 dB re 1 µPa, and aversive behaviour was seen at levels above 145 dB re 1 µPa (Lucke et al., 2009). Fish also exhibited aversive behaviour to avoid schooling near air guns, which is noted as the most likely source of physiological damage (Jorgenson & Gyselman, 2009). This, alongside the evidence submitted by most *in situ*

surveys mentioned, suggests that most organisms naturally displace themselves to avoid harmful noise levels. This should not only help protect from physiological trauma but also reduce stress, limit hearing threshold change and, hopefully, minimize behavioural changes. Dolphins not only had a lesser effect from air guns than expected, but two of three individuals even showed the ability to anticipate the noise and limit its impacts (Schlundt et al., 2016).

Although there appears to be much promising evidence that the threat from seismic guns is less prevalent than may have been thought, there is a lack of evidence of behavioural and acute physiological effects, i.e. changing breathing rate or reaction to rapid movement. The main other concern is that fish exposed to 206 dB re 1 μPa, in the range that could cause damage to auditory organs, would initially react but then some would continue to swim towards the direction of the source. The report acknowledges that this is visible from the camera, that fish appear fine but this actually provides no accurate detail of the health of the fish and any hearing damage incurred (Wardle et al., 2001).

1.2.3.3 SONAR

Sound navigation and ranging (SONAR) uses a range of frequencies to reflect back from objects to aid in navigation and object detection. Sound production at low frequencies is referred to as infrasonic and at high frequencies as ultrasonic. Much of the research on impacts of SONAR has focused on effects of military SONAR on mammals. There is currently debate as to whether military SONAR causes effects akin to decompression sickness (DCS), and whether acoustic energy aids the formation of gas bubbles within tissues or whether it changes behaviour of whales and disturbs the central nervous system (Jepson et al., 2003; Piantadosi & Thalmann, 2004; Talpalar & Grossman, 2004). This has led to concern from the SCUBA diving community about potential human impacts, with tests being conducted on rats to understand whether there may be a threat to humans. However, there is currently disparity between studies. Tal et al., (2015) produced data using rats suggesting that a combination of

pressure and high intensity sound can induce neurological damage, contrasting with an earlier study that found no effects (Shupak et al., 2003).

In a recent study, 12 sperm whales (*Physeter macrocephalus*) were monitored using data tags during exposure to Low Frequency Anthropogenic Sound (LFAS); 1–2 kHz, at 214 dB re 1 µPa at 1 m (Isojunno et al., 2016). Playback of recordings of killer whales (*Orcinus orcas*), a potential predator, at natural levels during ambient acoustic conditions (the experimental control treatment) caused the *P. macrocephalus* to cease foraging and change behaviour to a non-foraging, non-resting state. However, during LFAS exposure whales changed their behaviour at sound pressure levels of 131–165 dB re 1 µPa. In contrast, when exposed to a Medium Frequency Anthropogenic Sound (MFAS), both as a control and during an incidental exposure, foraging rates were not interrupted. The study suggests that LFAS leads to a loss in energy intake without immediate compensation.

Blainville's beaked whales (*Mesoplodon densirostris*) were the subject of testing when tagged with devices designed to record sound, movement and orientation with seabed-based hydrophones used to record their echolocations (Tyack et al., 2011). The experiment used multiple approaches in the naval ranges near Andros Island, The Bahamas. The outcome showed that whales would stay an average of 16 km away from any SONAR testing and would take 2–3 days to return following the end of the tests. Alongside the SONAR tests, playback of band limited noise and killer whale (*Orcinus Orca*) vocalisations, a predator of the beaked whales, were used. In all cases, the beaked whales ceased to echolocate and began an uncharacteristically long ascent. This draws a stunning similarity to the results shown by Isojunno et al. (2016), where the reaction to SONAR and predators inspire the same reaction and a cessation of foraging activities.

Blue whales (*Balaenoptera musculus*) have also been shown to alter behaviour, but over a much larger range. Focusing on the 1–10 kHz region, it was noted that SONAR was disturbing

behaviour of whales (Goldbogen et al., 2013). The most notable part here, aside from the larger range of frequencies where behavioural change occurred, was that the authors acknowledged more than just a loss of energy intake. Here the 2nd and 3rd order effects of individual fitness and population health were acknowledged as being potentially threatened. It is worthwhile considering the range from which whales are able to detect sounds, and the negative relationship it has with energy needed for survival, migrations and mating. Noise has the potential to select for individuals with tolerance to noise but less adaptation to other environmental challenges. Healthy, competitive males could be prevented from competing for females in season if disruption from anthropogenic noise leaves them recovering from lost energy intake. Despite the SONAR used in this experiment being significantly less powerful than military versions, this study found that the blue whales reacted in a similar manner to the other deep diving species where they ceased to forage, increased swimming speed and changed normal dive behaviour. Pilot whales (*Globicephala mela*) were also shown to surface in synchronization with the arrival of sound waves from SONAR pulses (Wensveen et al., 2015). It is positive to observe whales attempting to overcome the damaging effects of SONAR but the level of stress they are experiencing is still clearly stopping them from reacting in the most effective manner each time they are exposed. This could in turn be what drives mass strandings.

The effects of SONAR on fish has also been investigated. Rainbow trout (*Oncorhynchus mykiss*) were used in an acute exposure experiment, where sound levels in excess of those that would be produced by ships were played to ease identification of the damage that may be faced by organisms near SONAR devices. Sound pressure of 193 dB re 1 μPa, for exposure lengths of 324 or 648 seconds were used. The most notable outcome was an auditory threshold shift of 20 dB at 400 Hz, which could be considered to be unsurprising as much of the evidence presented here suggests that there is far more likelihood for a detrimental effect at frequencies <2000 Hz. Following the experiment there was no mortality or apparent damage to auditory or non-auditory tissues (Popper et al., 2007). An unexpected

outcome was that different groups of trout had varied results, suggesting intrapopulation variation, which may allow natural selection for acoustic tolerance in environments with a high exposure to anthropogenic noise, somewhat similar to the dolphins in the previously mentioned study by Schlundt et al., (2016). In a further study, rainbow trout were subjected to a similar follow up experiment alongside channel catfish (*Ictalurus punctatus*) and hybrid sunfish (*Lepomis sp.*) in Seneca Lake, NY. The same exposure times were used but with both LFAS, peaking at 193 dB re 1 µPa, and MFAS, peaking at 210 dB re 1 µPa. As with other experiments using SONAR, there was no acute physiological damage (Kane et al., 2010). In a separate experiment, the channel catfish received various levels of MFAS from mid frequency active transducers (Halvorsen MB et al., 2012). Each exposure of 2 seconds spanned 2.8–3.8 kHz followed by a 1 second tone at 3.3 kHz. This was repeated 5 times with a 25 second gap between each. The cumulative sound exposure level was 220 dB re 1 μPa^2 s. One group of subjects had an auditory threshold shift of 4–6 dB at 2300 Hz. The threshold shift returned to the baseline level after 24 hours alongside the unaffected remaining catfish and rainbow trout.

It is perhaps concerning that much of the work cited here is sponsored by the US Navy who are looking to expand their program of SONAR testing and may be downplaying the negative effects (Dalton, 2006). Unlike with the previous two anthropogenic sources mentioned, SONAR appears to have the largest consequences for marine species and further expansion of the SONAR problem may increase this anthropogenic threat. Where there are examples of limitations and controls for the sources, it does not seem to be present here, especially where its effects seem to be understood so poorly when it comes to deep diving mammals (Parsons et al., 2008).

1.2.3.4 Boat traffic

Boats contribute noise to the environment in a multitude of ways; hull slap, foghorns, engines and prop spin are just a few examples. The many individual sources each contribute to the

anthropogenic impact of shipping noise and are further diversified by the manner in which they affect the marine soundscape. This can be by changes in sea state, speed, number of propellers and boat length amongst other variables. In comparison to readings taken in 1966, the ambient ocean noise near Bermuda has grown by 2.8 ± 0.2 dB re 1 μPa (44 Hz band), or 0.6 dB re 1 μPa per decade, which will likely rise following the expansion of the Panama Canal (Sirovic et al., 2016), as well as the development of the Nicaraguan canal. According to World Ocean Review (Gelpke & Martin, 2010), since the 1950s, tonnage of shipping has tripled and with it the number and size of ships has grown too (Cullinane & Khanna, 1999), significantly increasing noise in the oceans. Over the course of 28 months in the Haro Strait, USA, the Automatic Identification System (AIS) identified 1,582 unique ships. During this time, a total of 2,809 isolated signals were picked up by hydrophones where the median received signal was 20–30 dB re 1 μPa above background levels; both at low and high frequencies (20–30 dB 1 $\mu Pa^2\ Hz^{-1}$ from 100–1,000 Hz; 5–13 dB re 1 $\mu Pa^2\ Hz^{-1}$ from 10,000–96,000 Hz). This means that many of these transmissions were overlapping with the frequencies used by the native killer whale (*Orcinus orca*) population for echolocation (Veirs et al., 2016). This is of particular concern as interruption of echolocation could be linked to stranding (Pacini & Nachtigall, 2016). The mean boat speed in the area was 7.3 ± 2 ms^{-1} (14.1 ± 3.9 kt). This had a linear relationship with source level, which increased at a rate of 2 dB re 1 μPa for every additional 1 ms^{-1}. Given that many ships can travel faster than this is, this may not be representative of how loud the oceans can become, especially around shipping lanes. A study of killer whales off the NW coast of America used tags with digital acoustic recording and laser positioning tags. Boats within 1000 m were identified using geo-referencing, with 42% of the variations from baseline ambient sound being due to boat speed. In addition, simple linear regression showed that average vessel speed and the number of propellers per vessel were the only factors that predicted for significant noise levels (Houghton et al., 2015). If the current trend of ships growing in size and numbers continues, this will further increase the levels of vessel noise in the ocean.

Over the course of 2006, a two month study assessed the frequency ranges of different ships while underway in a marine sanctuary located of the coast of Massachusetts, USA. A total of 541 vessels transited a total of 3,413 times. Cargo ships, tanks and tugs, consisting of 78% of the transiting ships, made 82% of total transits, with some making multiple passages. The average source peak frequency was 71–141 Hz, with the vessel specific average sound pressure contribution ranging from 158 ± 2 dB re 1 µPa for research vessels to 186 ± 2 dB re 1 µPa for oil tankers. The average received levels in high traffic areas was 119.5 ± 0.3 dB re 1 µPa (Hatch et al., 2008). Notably, oil tankers contributed twice as much acoustic power as cargo ships and one hundred times more than research vessels. Commercial shipping of goods and resources contributes the most noise around large ports, therefore making it an important factor to be considered during the planning of new, and expansion of current, ports; not forgetting the impact of the construction itself. Studies that have provided improved characterization of marine traffic contribution to the soundscape make it easier to model how shipping routes effect different areas of the ocean. This understanding may make it easier, when considering expansion of ports, to minimize adverse effects on marine fauna. Further studies in a range of marine environments should address how the underwater topography of the region affects sound propagation of anthropogenic noise. In combination with models used for marine spatial planning and data from oceanography surveys, it may be possible to create increasingly accurate computer models of acoustic disturbance, providing better planning and protection. A separate study identified that that bulk carriers contributed a different frequency range to tankers and container ships, 100 Hz versus 40 Hz respectively. The difference in noise impact between highest and lowest contributors was only 5dB; a container ship at 188 dB re 1 µPa against a chemical transport ship at 177 dB re 1 µPa. This is quite a small difference, especially when the ships differed in mass by 28 Kilo Gross Tons. In addition, the study identified that there was asymmetry of noise from passing ships, with the stern being 5–10 dB louder than the bow (McKenna et al., 2012). Although not explored, it is likely due to the location of the propeller at the rear of passing ships.

1.2.3.5 Impacts of noise on marine life

Response varies depending on the type of noise and whether the fish is a specialist or a generalist, but continuous noise was found to have little effect whereas realistic boat playback, with its varying amplitude and frequency, caused an increase in cortisol production. The top sound level that test species were exposed to, 156 dB re 1 µPa, caused temporary deafness in some fish (Wysocki et al., 2006). This study clearly demonstrates that boat noise is inducing the secretion of a steroid, in teleost fish amongst other species, is an adrenal system response to acute and chronic stress (Mommsen et al., 1999). The other key concern found in the study is that the level of sound that fish were exposed, 156 dB re 1 µPa, is causing a temporary lack of hearing in fish. This is unexpected as this outcome has not been seen in other studies exposing fish to substantially higher volumes. This may be because of the environment of the study, the study species, or a mix of the factors that made them more vulnerable. Nonetheless this study has identified a vulnerability previously unnoticed that holds significance given that the sound level required to cause this damage was more than 30 dB below that recorded from passing boat traffic recorded in other studies.

Intraspecific species variation also contributes to effects of anthropogenic noise from boats. An increased consumption of oxygen relative to mass during exposure of ambient and ship noise playback was shown in shore crab (*Carcinus maenas*) (Wale et al., 2013). The increase showed during single playback did not produce the same results for extended playback over a series of days, where there was no change in average oxygen consumption across the test subjects, but crabs receiving ambient noise play back increased oxygen consumption. This is detailed as the possibility that crabs exhibited a maximal response on first exposure, or that they habituated, becoming tolerant to the noise and the handling of stress respectively. There is an obvious life stage variation in response to anthropogenic noise, especially those that have a pelagic life phase, but few studies have investigated intraspecies physiological variations and susceptibility to stress. The response to playback of ship noise seen in crabs was similar to that identified in a stress response study in spiny lobster (*Palinurus elephas*).

P. elephas were exposed to playback of boat noise which induced an increase in locomotor activities, causing an increase oxygen consumption, as well as an increase is the haemolymphatic bioindicators associated with stressful conditions (Filiciotto et al., 2014). European sea bass (*Dicentrarchus labrax*) and gilthead sea bream (*Sparus aurata*) received a playback sweep of noise in the same band frequency as boat traffic. Like the spiny lobster the response was movement, noted as intense muscle activity, as well as a haematological response (Buscaino et al., 2010). All of these studies demonstrate that there are an array of marine species demonstrating both physical, in the form movement, and physiological, in the form of the haematological reactions, associated with stress.

Further evidence of the stress induced from boat noise can be deciphered from the behaviours linked to physical reactions. Three-spined stickleback (*Gasterosteus aculeatus*) and the European minnow (*Phoxinus phoxinus*) decreased successful foraging levels when exposed to ship noise playback, as well as showing an increase in startle responses. Both species had different responses, minnows spending time away from foraging through inactivity or socializing, whereas the sticklebacks continued to forage, but with far less success (Voellmy et al., 2014b). Atlantic cod (*Gadus morhua*) larvae were treated with regular or random boat noise alongside a control group with just ambient noise. Both groups treated with playback of boat noise showed reduced growth rates with the larvae exposed to regular boat noise using up the yolk in sac at an increased rate. The regular boat treatment group all had a smaller body, in both length and width, and were easier to catch in predator avoidance experiments, a fallout of the increase in rate of yolk usage. All fish still reacted to boat noise when treated following the study, suggesting that there was no long term adaption to the treatment (Nedelec et al., 2015). Playback tests such as this offer the ability to determine just how the boat noise from passing traffic effects fish of all life stages. It should always be remembered that playback does not carry with it the physical action of a boat passing by, which may mean that the effects seen in tests such as these may be reduced when compared to the effects of an actual boat pass. Much like where lab tests lack the physical passing of a boat, species kept in laboratories

should be healthy. This will not be the case in wild populations as there will likely be a variety of pathologies within the population. This key consideration has been addressed where varied levels health caused a differing physiological response by European eels (Anguilla anguilla). Healthy and poor condition eels were treated with playback of ambient coastal noise as well as ambient costal noise with passing ships. The healthy eels showed no change in behaviour whereas those in poor condition exhibited increased ventilation rates and a decrease in startle reaction to a predator stimulus (Purser et al., 2016).

The physical impact of boat traffic, however, has been monitored in some studies on wild populations. Displacement of bottlenose dolphins (*Tursiops truncatus*) was noted off the coast of Croatia due the intensity of tourism and leisure based boat traffic (Rako et al., 2013). Far from just a displacement issue, in the same area, dolphins were found to adjust whistle frequency conversely to the anthropogenic noises found around them (Rako Gospić & Picciulin, 2016). The Gulf of Mexico was used to test Digital Spectrogram recorders alongside a computer algorithm designed to detect boat traffic at natural and artificial reefs. The study identified more visits at artificial reefs than natural ones, and that deeper reefs (>25m) suffered the least seasonal variation in visits (Simard et al., 2016a). This technique, minus set up cost, could provide a cheap way to monitor individual vessels entering marine protected areas as well as the impact they are having. It could be used to provide information for planning in areas where noise is a concern, such as shipping lanes, or areas designated for protection, such as MPAs. The study also shows that fish on reefs are just as much exposed to traffic as those in shipping lanes. This is particularly important, as coral reef fish larvae are less likely to settle on reefs with areas of boat noise (Simpson et al., 2016a). When brown meagre (*Sciaena umbra*) were treated to boat noise in a field study, within a protected area, there was an identified increase in behaviours associated with anti-predation, flight and hiding. There was no difference in level of fish activity and sound level and all behaviours normalised quickly following exposure (La Manna et al., 2016). In addition to causing stress, boat traffic can inhibit communication between multiple fish species. Damselfish, brown meagre and red-mouthed

goby (*Chromis chromis, Sciaena umbra* and *Gobius cruentatus,* respectively) had auditory sensitivity determined in lab conditions to determine the effect of traffic around an MPA near Trieste, Italy. The impact of a passing cabin cruiser substantially reduced auditory threshold, including the range that test species used to communicate (Codarin et al., 2009). Communication is used for a variety of tasks including socializing and predator avoidance. Masking by boat traffic noise is less than desirable in MPAs that are designed to protect, and even promote, sustainable ecosystems. *Gobius cruentatus* and *Chromis chromis* were subsequently studied in situ with playback of a 26 m passenger ferry and 5 m fibreglass hulled boat. Although there was no immediate behavioural change established, a time-budget analysis revealed that *C. chromis* spent less time maintaining their nest while *G. cruentatus* spent less time in the protection of their den (Picciulin et al., 2010). The short term impact of the playback appears minimal for both species, but outlook for life span and egg fecundity is concerning. If hearing was disturbed enough, it may have been harder for subjects to identify approaching predators (Simpson et al., 2016b).

When compared, reefs broadcasting boat noise versus ambient reef noise, the former showed a substantial reduction in settlement of fish (Simpson et al., 2016a). Post-larval southern rock lobster (*Jasus edwardsi*) were shown to have a reduced positive taxis towards reefs in windy conditions due to the impediment that the conditions caused on their ability to detect the reef sound (Hinojosa et al., 2016). As a comparison, the detrimental effect of wind noise would be substantially less than that of boat noise, therefore it could be expected that the same effect would occur if lobster were exposed to boat traffic, even if the latter noise may be more fleeting.

Aside from the direct impact of boat traffic on the marine environment, it is important to acknowledge that the supporting infrastructure of ports also contribute to the effects of anthropogenic noise. Roads are one of the key forms of ingress and egress on land for any port and are often heavily trafficked. A study set in waters surrounding a road bridge identified

that blacktail shiner (*Cyprinella venusta*) had undergone a detrimental effect on communication because of the lack of propagation of their calls (Crovo et al., 2015). Although this is just an example from one study, it is also important to acknowledge that only a limited number of sources could be reasonably covered and that there are other major contributors of anthropogenic noise in the marine environment not covered here such as: offshore oil platforms, wind farms, dredging, aquaculture and fishing; including the effects of alarm systems designed to discourage approach of species not designed for capture. The research referred to here covers an immense range of subjects, both providing positive and negative insights to the effects of anthropogenic noise. It is not, however, a standalone threat to the inhabitants of the marine environment.

1.2.3.6 Not the only threat to hearing.

The damage caused by anthropogenic noise itself mostly aligns with behavioural changes, hearing shifts and acute physiological reactions. There is however, an emanating threat from ocean acidification. Increased acidity of the ocean can have a detrimental effect on behaviour. Juvenile clownfish (*Amphiprion percula*) no longer avoided reefs in a CO_2 rich environment akin to that predicted for the oceans in the future (Simpson et al., 2011b). Young clownfish would find themselves vulnerable to predation if approaching a reef. Larvae of catadromous fish species (barramundi, *Lates calcarifer*) were treated with the same conditions to find that they were repelled by the noise of a habitat to settle in, where they would normally show a positive taxis within 3 days. The larvae also exhibited reduced swimming speeds, heightened anxiety levels and a fast onset of metamorphosis (Rossi et al., 2015). The negative effects of slower swimming speeds and heighted anxiety leads to a waste of resources for growth and taxis, whilst potentially choosing a poor choice of habitat for settlement in waters with increased acidity. If this is coupled with the masking of healthy environment by anthropogenic noise, this could vastly damage reef recruitment. In fact, with the effects of ocean acidification and changes to reef soundscape, even larvae not treated to increased CO_2 levels in the water found it difficult to navigate to areas to settle (Rossi et al., 2016). Otolith size has been

attributed with change due to increase in ocean acidity, with increase in both mass and density leading to increase hearing levels. This may seem a benefit but as the previous evidence shows, it seems to cause confusion when larvae orientate themselves to navigate to a suitable habitat (Bignami et al., 2013).

1.2.3.7. The importance of sound to fish.

Sound provides marine organisms with cues for orientation and habitat selection, a sensory ability to avoid predators, as well as a method of both intra and inter species communication. From the first few days of life to the last dash away from a predator, hearing is a vital asset to marine life. Thus far this text has focused on the negative effects of anthropogenic noise and the impact it has upon marine creatures. Here, the aim is to elaborate on the evidence supporting the use of sound by marine creatures and the importance that the marine soundscape remains as undisturbed as possible.

Ambient noise is temporal and its effects are vital for sustaining income of juveniles to a reef population. It has been assessed that the two main contributors to ambient reef noise are snapping shrimp (*Alpheidae*) and sea urchins (*Echinodea*). Short term peaks in reef noise are indicated by dusk and the arrival of the new moon, while longer term sound increases are found during summer when compared to winter. Despite the temporal differences, there were contributions from 100–15,000 Hz with sound reaching almost 150 dB re 1 µPa (Radford et al., 2008). Similar noise patterns to the snapping shrimp and sea urchins were identified in fish who contributed to reef acoustics with a dawn and dusk chorus. This diurnal pattern was identified in seven fish choruses with energy between 50 Hz up to more than 4 kHz. There was evidence of frequency and temporal segregation between species in some cases but not all (Parsons et al., 2017). Not all discourses are restricted to being part of a diurnal chorus, and fish are able to use vocalizations to communicate with one another in a variety of ways. A study by Tricas and Boyle (2014) used acoustic and video recording to create a sound library of vocal species in Hawaii, USA. Long term monitoring was found to infer periodic reproduction

activity and population changes. Of the 96 species present, 45 were recorded producing a total of 85 sounds covering a range of behavioural interactions. Agonistic interactions, resource defence, reproduction, nest defence, feeding and feeding related behaviours were all identified. Most sounds were in the frequency range of 100 Hz to 300 Hz with the exception of feeding events. Feeding associated sound, mostly associated with parrotfishes and triggerfishes, was recorded at higher frequencies of 2–6 kHz as their teeth scraped against benthic substrate (Tricas & Boyle, 2014). The agonistic behaviours consisted of aggressive interactions, mostly with conspecific individuals over reproduction or food, territory defence and nest defence. Reproductive interactions were identified as courtship or spawning. Vigilance was one of the most common sounds recorded, both in the number of times vocalizations occurred as well as the breadth of species producing the sound. This vital communication allows organisms to alert each other to the presence of predators. This carries particular importance as other evidence has shown that exposure to anthropogenic noise can interfere with startle reaction as well as reaction to predator sound (Voellmy et al., 2014a; Simpson et al., 2016b). This wide variety of interactions across so many species shows how important an undisturbed ambient acoustic environment is for marine life. Although this paper does not manage to record all of the species known to vocalize in the area, as some vocalizing species rarely do so, all those in the area will still react to sounds produced by other species to guide their decision making. Not all contributions to the soundscape by marine organisms are direct and deliberate, they may be incidental but no less relevant in their input to the ambient sound. Using hermit crabs (*Clibanarius diugeti*) to corroborate findings of a field study, benthic invertebrates were contributing to a sound pressure increase of 4.6–6.2 dB re 1 µPa across a frequency range of 11–17 kHz by incidentally scraping their hard shell when moving at night (Freeman et al., 2014). Incidentally, this is an example of a particularly high frequency sound level akin to that of the parrotfish and triggerfish recordings produced by Tricas & Boyle (2014).

All of the above contributions to reef noise create the “sound print”, which is vital for maintaining good levels of reef recruitment. Using evenly spaced artificial patch reefs with alternating playback of reef sound between no sound and reef sound, it was shown that there was significantly more recruitment to the reefs from which a natural sound was emanating. Further to this, when exploring variations in frequency of reef sound, those with either a high or a low frequency of reef sound were preferred by settling fish to reefs that produced no sound at all. Of those reefs with play back, different species were found to prefer to recruit to patch reefs with a higher or lower frequency. The most compelling evidence of the significance of undisturbed reef noise is that two important taxa, *apogonids* and *pomacentrids*, made up 95% of recruitment during this test (Simpson et al., 2004). Where the previous study found certain species show preferences towards certain frequencies of reef noise to identify an appropriate reef habitat to settle in, some have a polar reaction. Selection strategies were shown to have either direct selection of habitats due to their sound production or a selective avoidance of them (Parmentier et al., 2015). The recruitment driven by noise, whether it is a positive or negative reaction, will act as an effective guidance over a long distance as a particle motion assessment within fish auditory range was able to determine that reef noise would be heard kilometres away from its source (Montgomery et al., 2006). This demonstrates the distance from which organisms in their pelagic life phase are able to use sound as a navigation tool and how important it is that sources are not impeded. The extensive distance of which the sound from reefs are able to propagate is not limited to the use of vocal species. Temporal sound detection in fish is equal between those who produce sounds and those that are not vocal. Shown using species from *otophysines* and *anabantoids* taxa, fish could determine separate clicks with less than 1.5 ms separating each individual sound (Wysocki & Ladich, 2002).

1.2.3.8.1 How to solve the problem – planning, prediction & management

A tool based on SPreAD-GIS has been developed with the use of GIS (Geographic Information System) to aid in the mapping of noise propagation in natural ecosystems. SPreAD-GIS is

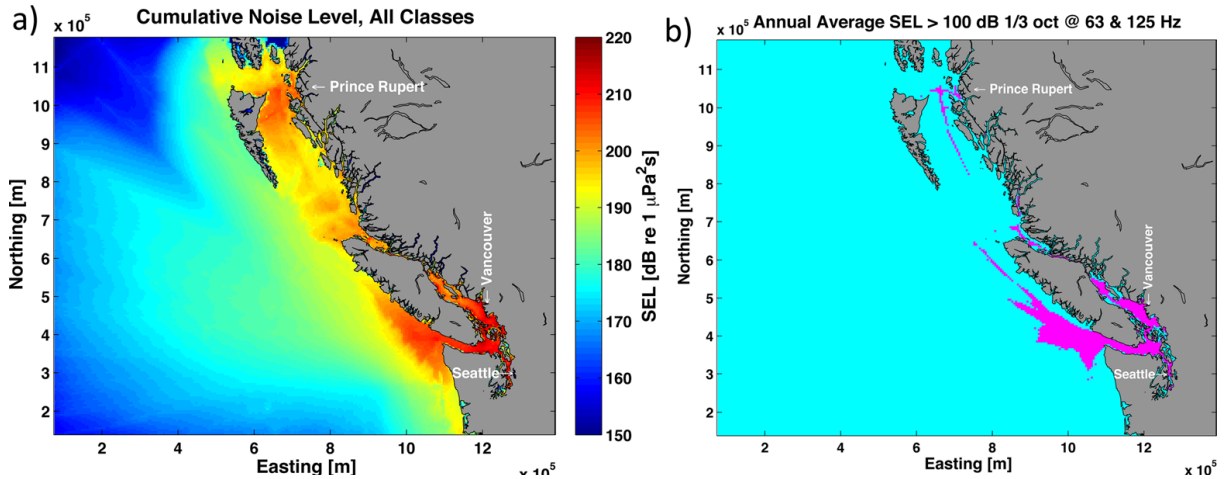

Figure 1.5 – Sound levels in Canada's Exclusive Economic Zone (west coast). (a) Cumulative sound exposure level from vessel traffic from Jan to Dec 2008. (b) Areas where the estimated annual average sound pressure level (SPLrms) exceeded the EU Marine Strategy Framework Directive of 100 dB (SPLrms) in 1/3-octave bands centered on 63 or 125 Hz. Figure from Erbe et al., 2012.

able to take into account the influences of anthropogenic noise compared to the ambient noise and can be inclusive of variations due to weather (Reed et al., 2012). It is not noted whether this could be extended to the marine environment, but the theory shows that it could be practically possible. Spectral source levels from shipping in the St Lawrence Seaways, an area mentioned in previous studies for effect of shipping noise on the whales that inhabit the area, were monitored for a year from November 2012. The study enabled the geographic and temporal modelling of shipping noise variability. This allowed for further investigation onto the effect of shipping on local organisms as well as planning for the mitigation of anthropogenic noise in the vicinity (Simard et al., 2016b). A similar study inclusive of a larger area, covering Canada's exclusive economic zone, considered cumulative noise alongside the use of AIS (Automatic Identification System) data. It determined that sound levels, in an area important for killer whale conservation, were above that determined to be exceeding limits of "good conservation status" as set out by the EU Marine Strategy Framework Directive (Tasker et al., 2010). The analysis showed that it was possible to use the information for improving noise management in the conservation area (Erbe et al., 2012)(*Figure 1.5*).

AIS was used once again along with a single hydrophone to conduct cumulative noise modelling as well as characterization of temporal ship noise to prioritize mitigation of ship

noise in waters around Falmouth, a busy port and naval base in the United Kingdom (Merchant et al., 2012a, 2012b; Merchant et al., 2016). These studies are evidence that it is possible to predict the impact of sound in environments that may become or are already influenced by anthropogenic noise. Use of this evidence could enable future port, marine and costal projects to mitigate the acoustic impact they have on the surrounding environment.

Aside from looking at the best way to protect the environment, it is possible to be proactive and mitigate the noise from shipping prior to it ever reaching a port. Using CFD-based URANS hydrodynamic prediction alongside the Ffowcs-Williams Hawkings equation for noise propagation, a study was able to accurately predict the noise production of a LNG ship prior to production (Kellett et al., 2013). If this method was routinely applied to the design phase in the construction of all future marine vessels, noise distribution from shipping could be significantly reduced and minimum standards to achieve could be set for vessels to be legal. Shipping areas could then be controlled by levels of noise pollution encouraging companies to invest further in reducing their anthropogenic noise impacts if it would allow them greater freedom of navigation. More than just protecting the environment, reducing noise could also save the shipping industry billions of dollars in tackling biofouling. Vessel noise was shown to give a significant increase in settlement of biofouling species on the hull of ships (Stanley et al., 2016). Therefore, by using quieter ships will protect marine species from anthropogenic noise exposure whilst saving shipping companies money on cleaning ships and fuel, as drag will be reduced from the decrease in biofouling. An important consideration pertinent to this study is that it shows some species are able to adapt and survive alongside boat noise. Whether it is adapting to survive alongside it or moving away from it, some species are finding a way. It has been suggested that the isolation of boat traffic is the reason for wind farms having increased levels of some species seen around them (Inger et al., 2009). However, this should not reduce from attempts to protect the marine environment due to other pressures already leading to disruption to species home ranges (Harborne & Mumby, 2011; Simpson et al., 2011a; Milazzo et al., 2013;).

Pre-emptive planning and monitoring noise output could be supported by live population monitoring, a vital part of conservation. Doing this is often limited by the ability to physically site species of interest. Passive acoustic monitoring could be useful for these species and even those that are easily identified due to the range it can offer. Automation can enable studies to leave detectors in hard to reach places and can occur without the constraints of time or weather that may deter human endeavour. This can be achieved by towed sensors, or by static ones, and can target any marine acoustic taxa (Marques et al., 2013). Passive acoustic monitoring such as this can now be assisted with the use of computer analysis using MATLAB and R. This progress should enhance understanding with better analysis of biological sound and the effects of anthropogenic noise on a spatiotemporal scale (Merchant et al., 2015). There are further examples of the use of static recorders. Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*) were monitored using passive acoustic detection. This enabled detection, counting, localizing, and tracking of individuals. The study acknowledges the importance of the contribution to important conservation data, stating that distribution, abundance, ecology, and behaviour are essential for conservation (Li et al., 2010; Kimura et al., 2010). Small data loggers were used to monitor Baltic populations of harbour porpoise (*Phocoena phocoena*). Working alongside visual monitors, it produced a reliable method of monitoring local populations with a reduction in the intensity of work required to solely visually monitor the species (Kyhn et al., 2012). Leopard seal (*Hydrurga lepton*) monitoring via acoustic sensors could identify areas that were critical to the species that traditional monitoring had not. The passive acoustic monitoring arc of 4225 km was able to monitor populations accurately and is noted as a genuine alternative, especially useful for more remote areas (Rogers et al., 2013). Further to just identifying specific species, recorders can be used to monitor whole reefs. A hydrophone array spread across seven locations monitored biological sound for its spatial, temporal, and spectral properties in an environment free of anthropogenic influences. Refinement of sounds by triangulation and focusing enabled

the study to identify that the majority of sound production of organisms in the area came from within, or in the immediate area of, surrounding reefs (Freeman et al., 2014)

Planning and prediction doesn't just apply to locating and monitoring populations but to understanding and reducing anthropogenic input. Where the use of bubble screens has already been mentioned, some studies are aiming to better identify how pile driving affects its surrounding environment by accurately mapping it with the use of a three-dimensional vibroacoustic model. This model identified that the near-field response in the water column of mostly conical waves exhibited from the pile after hammer impacts, vertical polarization of waves from the seabed and Scholte waves at the water–seabed interface (Tsouvalas & Metrikine, 2013, 2015a, 2015b).

It is also important to acknowledge that where renewable energy is being steadfastly developed, a group of 20 nations has formed the Ocean Energy Systems collaborative intergovernmental agency, where one of its 3 key goals includes the understanding the effects of underwater sound from marine energy devices as they are developed (Copping et al., 2014). Some of the data included in this work acknowledges that the main noise contributed was during construction where harbour porpoises were displaced, but operation of the equipment did not have the same effect.

1.2.3.8.2 How to solve the problem – Marine Protected Areas

Marine protected areas have been imposed across the globe with many bodies around the world creating legislation to protect the ocean. Although this has sometimes led to conflict between stakeholders, there are attempts to change this to further enable their creation (Boyes & Elliot, 2014). There are multiple factors considered to create MPAs, with software being a useful tool to aid design. Anthropogenic noise can be overlooked when considering other more obvious biological variables or anthropogenic threats. Many of the papers mentioned in this text were studies located within MPAs yet were noting detrimental effects of

anthropogenic noise on the area's inhabitants. Specificity is also important, understanding how the species you wish to protect are being affected, be it a detrimental effect on predator avoidance or a struggle to communicate. This is a vital consideration for species protection and a prominent consideration for the second data chapter of this study.

1.2.3.9 Summary

The notable trend in the papers referred to above is that low frequency noise appears to be the lead cause of stress from sources of anthropogenic noise in the marine environment. Chronic physiological damage does not seem to occur, even when individuals are exposed to levels in excess of those that would be experienced. Much of the research, however, focuses on acute effects on marine mammals, while comparatively little work studies fish species. Often the work that has focused on fish has concentrated on a single species, with little or no consideration being given to the effect on the population as a whole. The sources of anthropogenic noise focused on in much of the research to date also leaves crucial knowledge gaps, with most studies looking into large and high impact sources of anthropogenic noise, with far fewer focusing on the smaller more consistent contributors such as small boat traffic. This study endeavours to bridge this gap, with a focus on chronic boat noise on whole populations.

1.3 Study aims and objectives

This literature review has highlighted how important coral reefs are to a range of species, yet how the vital area of coral reef flats remains understudied. The literature review also exposed knowledge gaps in the effect of chronic boat traffic from small vessels on whole communities, while highlighting the broad danger that is posed to the marine environment by many sources of anthropogenic noise. Chapter 2 presents a study designed to test the importance of the habitat of coral reef flats to settlement of *Stegaste*s spp., as well as their interaction with the large populations of *Haemulidae spp.* also found on the patch reefs. Chapter 3 presents a study designed to test the effect of chronic boat noise on communities as a whole. The aim of this research as a whole was to identify important community relationships in coral reef flats of Cape Eleuthera that may have wider effects on reef health, whilst determining how anthropogenic noise effects these communities.

2. Interactions in habitat occupation by *Stegastes spp.* and *Haemulidae spp.* at Cape Eleuthera in The Bahamas.

The Cape of Eleuthera offers a protective body of water with the perfect nursery conditions for *Haemulidae spp.,* amongst others*,* as well as providing a permanent home to many species including the *Stegastes* genus. This study set out to determine if the *Stegastes spp.* found in the Cape of Eleuthera occupied separate niches and if the genus had any relationship with the *Haemulidae spp.* using the reef system as a nursery. The results of this study indicate that the species present from the *Stegastes* genus have overlapping niches that have caused competitive exclusion, the development of a hierarchy and influenced the settlement of *Haemulidae spp*. While all *Stegastes spp.* occupy reefs with a similar structure of substrata to enable escape from predators, size and location of territory both vary. Dominating the higher sections of patch reefs, holding the largest territories and being able to dive amongst the schools of *Haemulidae spp.* for cover, the longfin damselfish (*Stegastes diencaeu*s) has clearly competitively excluded the other *Stegastes spp.* from the most suitable territories. The bicolour damselfish (*Stegastes partitus*) is left to establish territories on less populated reefs, but without the competition from *S. diencaeus* the species is still able to control the idyllic tops of these alternative patch reefs. The beaugregory damselfish (*Stegastes leucostictus*) has been forced to find its own niche either lower down on patch reefs occupied by other *Stegastes spp.*, using the *Haemulidae spp.* schools to protect itself, or occasionally occupying isolated patches. This hierarchical relationship amongst the *Stegastes spp.* then shapes the transition of *Haemulidae spp.* through the nursery, with the *Haemulidae* family most commonly found on the reefs alongside *S. diencaeus* and *S. leucostictus*.

2.1 Introduction

Competition for survival exists throughout the marine environment, be it for food, territory or reproductive success; or a combination of these factors (Potts, 1977; Hughes et al., 1987; McCormick, 2016; Ryabov et al., 2017). This competition drives different species into separated niches, and even within species it can cause individuals to change behaviours in order to survive (Svanbäck & Bolnick, 2007).

Coral reefs are heterogeneous habitats, fragmented into semi-isolated islands, each with their own individual community. Like any other marine habitats, there are many examples of overlapping niches leading to competition for resources (Bouchon-Navaro, 1986; Pratchett, 2005). The varying ecology of these reefs often depends on their location and size. Fore reefs are populated by larger adults while smaller patch reefs act as intermediate habitat after juveniles have departed the safety of the seagrass beds and mangroves (Nagelkerken et al., 2002; Nagelkerken & van der Velde, 2003). These nursery habitats are important for the healthy function of the larger reefs (Harborne et al., 2006).

An important characteristic of these patch reefs is the protection that holes in the structures provide from predators, as well as strong currents for small fish (Hixon, 1991; Johansen et al., 2008). The crevasses within a reef also provide shelter for nesting and foraging (Robertson & Sheldon, 1979). The protection and height of the benthic structure provided by a reef then creates a hierarchy competing for the best location, where *Stegastes spp.* will exclude other marine creatures (Harborne et al., 2011). Aside from other species, some *Stegastes spp.* will out compete others within their genus for optimal territories, with *S. planifrons* competitively excluding *S. leucostictus* in the Indian Ocean (Ebersole, 1985).

This study investigates the competitive interactions between *Stegastes spp*. Focusing on adults of several species in the *Stegastes* genus, this study aimed to identify the drivers of

territory selection within the expansive system of patch reefs in Cape Eleuthera. The study tested whether species within the genus had a homogenous settlement choice, or whether there is interspecific variability. Further, this study tested whether there was an interaction with the *Haemulidae spp.* populations that affected the settlement of *Stegastes* species.

2.2 Materials & methods

2.2.1 The study site

This study was conducted during June 2015 off the coast of Cape Eleuthera, The Bahamas (N 24º50'05", W 76º20'32") (*Figure 2.1*). All of the sites used during the study were found in the waters encapsulated by the Cape of Eleuthera, where there exists a system with in excess of 200 patch reefs. From these 200 candidate patches, those that had *Stegastes spp*. populations identified in previous surveys were compiled. To eliminate anthropogenic noise as a variable, reefs located in areas often frequented by boat traffic were also removed from the list. This coincidently removed those reefs that were influenced by high tidal flow rates (*Figure 2.2)*. From the remaining reefs, study sites were then selected at random. A total of 7 separate patch reefs were surveyed during the study, each of which had multiple *Stegastes spp.* within the community that existed at the site. All of these reefs were situated in water with a depth between 2.7 m and 3.7 m.

2.2.2 Variables

The intent was to gather data on the physical structure of the territory of each *Stegastes spp.* individual to identify if each species within the genus had its own niche, whilst simultaneously ascertaining if the large number of *Haemulidae spp.* had an influence on the territory selection of *Stegastes spp.* or vice versa. To achieve this, a range of biotic and abiotic characteristics needed to be collated.

The scope of the abiotic variables was to characterise the physical components of the territory each individual *Stegastes* occupied. This was recorded using 6 variables. The two largest

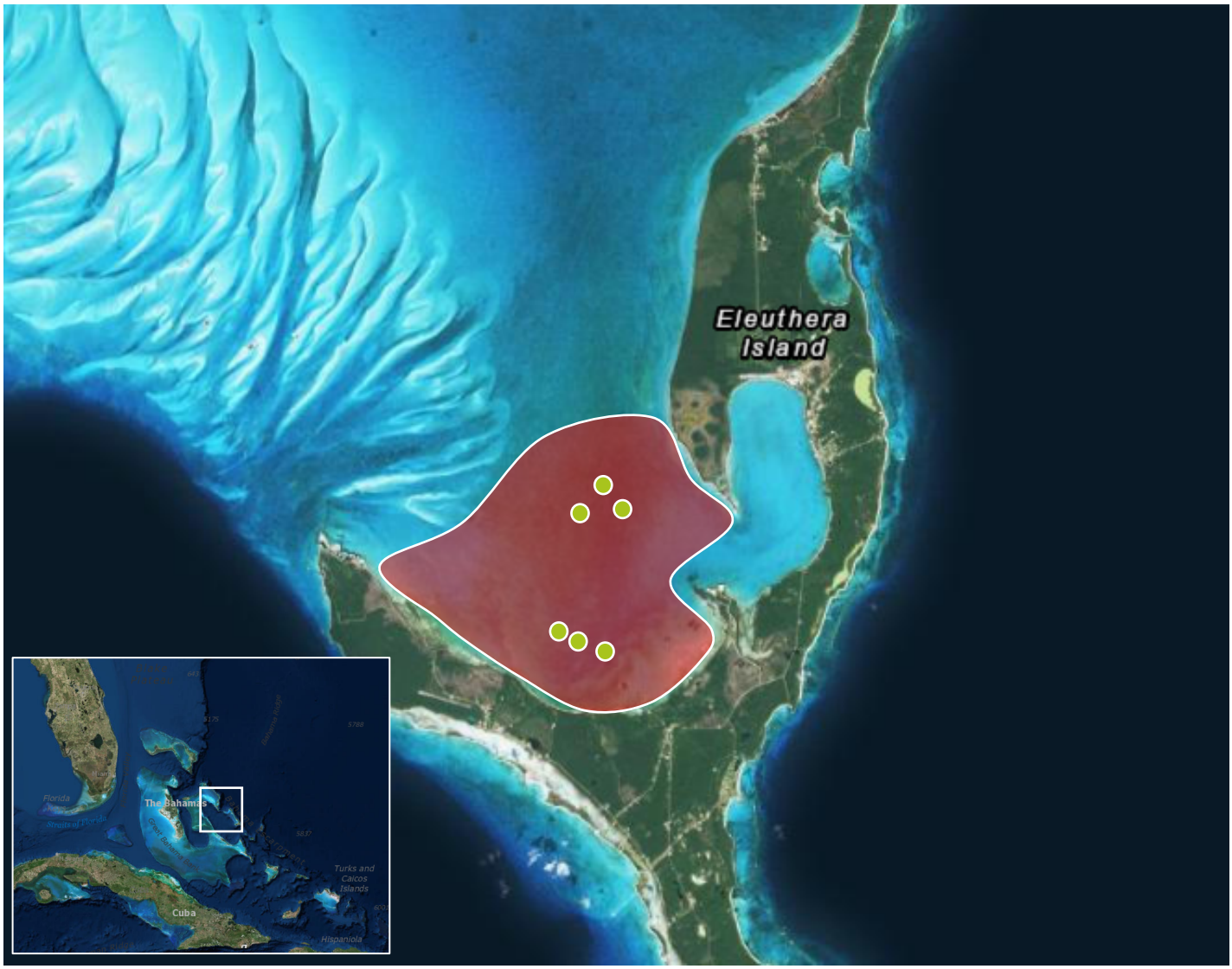

Figure 2.1. Field site with boundaries of study locations marked. Bottom left: The location of Cape Eleuthera to the northeast of the Caribbean, bordering the Atlantic Ocean. Central image: The Cape of Eleuthera. The nursery patch reef system, identified in red with a white border, is protected by the island of Eleuthera and a series of sandbars to the north. Within in this patch reef system are six yellow-green circles, each identifying a survey site - with the exception of Harrin and Harrin MkII which located to closely to distinguish in this image. The bottom three from left to right are: co-located Harrin and Harrin MkII, C4 and FWA. The top three from left to right are: 57, Esther and Tiny.

perpendicular widths were measured to provide an estimate of the overall area consumed by individual *Stegastes* territory; these data are referred to as the widest width and the widest perpendicular width. These data represent, and are referred to as, each individual *Stegastes'*

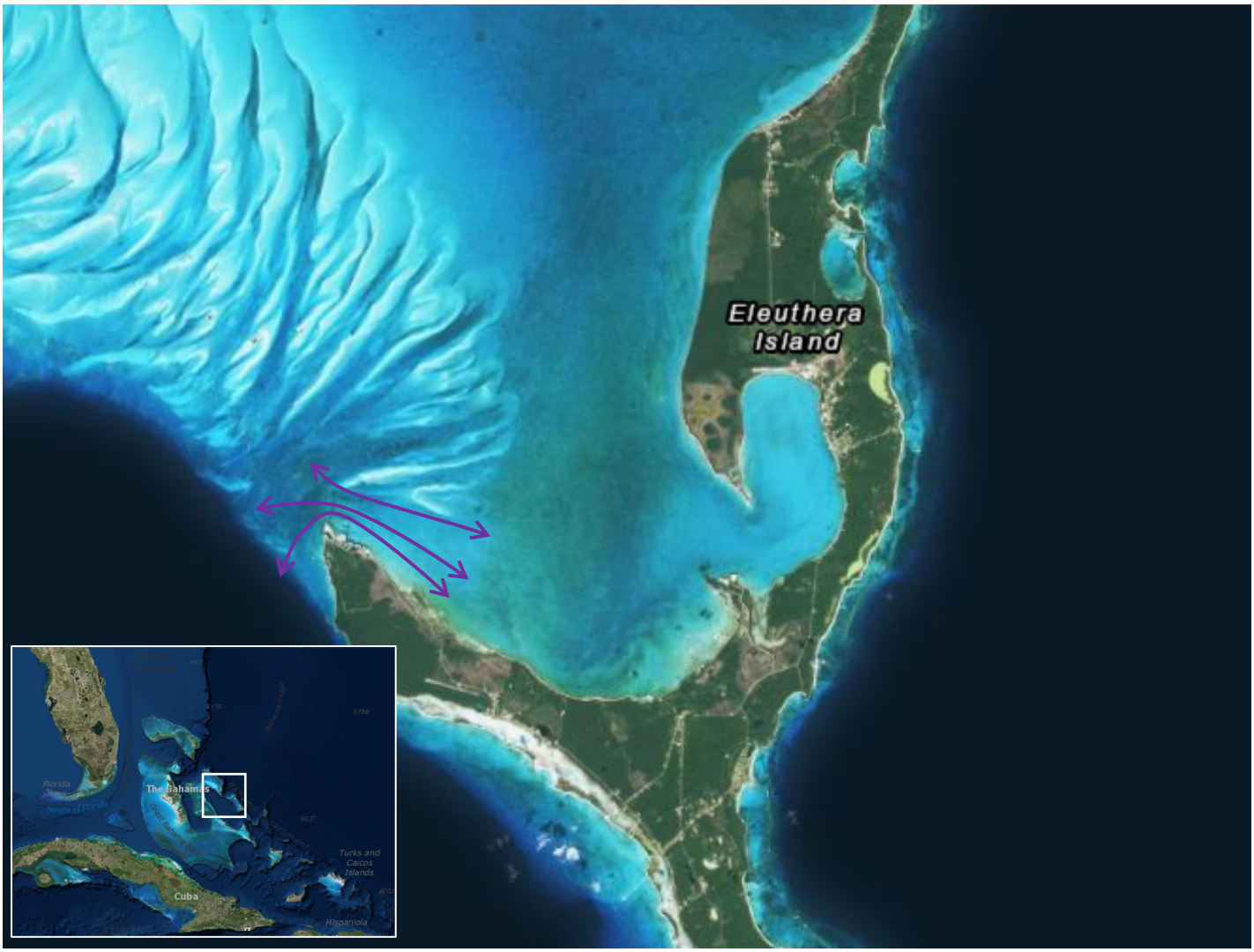

Figure 2.2. High tidal flow rate near Cape Eleuthera. Purple arrows show the area affected by high tidal flow rate due to the tide being canalised by sandbars to the north.

territory size. They were not, however, combined to provide a data set representing area, or combined with the measurement taken of the height of the reef to give a 3 dimensional representation, as the physical structure of the substrate was polygonal in nature. Depth was another variable taken at each site, with all surveys being conducted at the same point in the tidal cycle to ensure parity. The height of the reef from the sea bed was also recorded at the highest point of each patch reef. The remaining two physical characteristics that contributed to this data set were the number of holes within the substrata, and the average width of these holes, within an individual's territory. Holes within a reef can provide escape routes from

predators, so it was considered that this may be a factor in which may shape selection of territory by *Stegastes spp* (Harborne et al, 2011).

Two of the biotic variables were closely linked to the abiotic variable height of the reef. These data, height of Stegastes spp. from the sea floor and height of Stegastes spp. relative to the reef, were recorded to enable the study to determine if there was a correlation between the species and where it located itself on a reef. The decision to include this variable was related to evidence form previous papers stating a hierarchy between species meant that the dominant species selected territories at the top of the largest reefs as this provided a dominant view point over the surrounding area (Harborne et al, 2011). Once the height of the reef and the height of the individual was recorded, the latter was divided by the height of the reef to provide a data point that considered where relative to a reef and individual occupied, regardless of the total height of the reef. The other two variables considered were both relating to the number of *Haemulidae spp*., after an abstract observation had noted that often, it appeared, that certain *Stegastes spp.* did not co-exist with the large populations of *Haemulidae spp.* This is particularly due to the large number of *Haemulidae spp.* that exist in the study area, using the patch reef system as a nursery. The first variable was the number of *Haemulidae spp.* within the immediate vicinity of the *Stegastes spp.* territory, this was considered to be those found within 1 m of the home range of an *Stegastes spp*. territory. The second variable was the number of *Haemulidae spp.* swimming around the whole patch reef. The breakdown into these two groupings was due to how *Haemulidae spp.* schools swam around a reef. The presence of large numbers of Haemulidae spp. did not guarantee that all areas of the patch reef would be smothered by the species, in particular the tops of the reefs were often clear of the family as schools tended to stick near to the sea floor and only go over the top of the smallest reefs. Therefore these variables were intended to determine if *Stegastes spp.* could exist surrounded by schools of *Haemulidae spp*., exist on reefs alongside *Haemulidae spp*. but not immersed in the family, or would not coexist at all.

2.2.3 Survey

To minimise the influence of anthropogenic noise, survey vessels approached at less than 10 knots, or 1200 RPM, once within 250 m of a focal reef. Routes to and from sites were planned in advance to avoid travelling within 250 m of any other study site. Once within approximately 100 m of the reef, the flow of the tide would be identified so the boat could be positioned to drift towards the reef with the engine being idle, further reducing disturbance. Once the anchor was set, the boat would settle around 50 m from the reef when the engine would be cut and a short soak period, approximately 2 minutes, left before surveyors entered the water.

The territories of all the *Stegastes spp.* occupying the patch reef were identified and observed from a distance of at least 5 m in order to determine the extent of each individual's territory. The number of *Haemulidae spp*. inhabiting the area surrounding each *Stegastes spp.* territory, as well as the total population of *Haemulidae spp*. that inhabited the patch reef as a whole, were also calculated from this observation point. All of these measurements were recorded for each of the *Stegastes spp.* occupying the patch reef prior to any invasive measurements being taken, to minimize disturbance to the survey species and ensure that all measurements taken were representative of each individual's territory. The population of the *Haemulidae spp.* was calculated by taking a group average for both the total number of the species present across the patch reef as well as for those in the immediate vicinity of each *Stegastes*' territory. Those fish in the immediate vicinity were defined as within 1 m of the outcrop of reef that the damselfish occupied. Where an individual's territory was not easily identifiable initially, a prolonged period of observation would provide clarity. Due to the short time period over which the data collection for this study occurred, there was almost no variation in time, tide, weather and visibility. This enabled consistency in the distance from which the initial observations were recorded. After the variables that could be recorded at a distance were complete for all individual's, the more invasive physical measurements recorded were made by a pair of researchers diving by snorkel to avoid incidental disturbance by SCUBA noise. Pairs used transect tapes to record abiotic measurements noted in the sub chapter 2.2.2. Any territory

containing more than 10 holes had the full number counted, but only 10 were measured to contribute to the average hole size as it was deemed this would give a sufficient reliability to the average whole size data.

2.2.4 Statistical analysis

None of the *Stegastes spp.* occurring within the patch reefs were excluded during data collection (*Table 5.1*). Once the data set had been compiled, however, several *Stegastes spp.* had either not been identified during data collection, threespot damselfish and cocoa damselfish (*Stegastes planifrons* and *S. variabilis)*, or were inconsistently surveyed and therefore unable to provide enough data for accurate analysis, dusky damselfish (*S. adustus*). Thus, the decision was made to continue with the three species that had larger numbers of individuals surveyed: beaugregory damselfish (*S. leucostictus*), bicolour damselfish (*S. partitus*) and longfin damselfish (*S. diencaeus*).

One-way Analysis of Variance (ANOVA) tests were used to test for significant differences between the three species, *S. partitus, S. diencaeus, and S. leucostictus,* for each of the recorded variables. Statplus software was used to complete the One-way ANOVA tests. Following this, Multi Factor Analysis (MFA) was used to consider the relationships between all of the variables (XLStat). For all of the statistical analysis, only the 30 individuals from the three species recorded in larger numbers were used (*S. leucostictus*, *S. partitus* and *S. diencaeus*).

2.3 Results

Out of the seven study sites, *S. partitus* appeared on four patch reefs. On three of these four reefs, *S. partitus* was the only *Stegastes spp.* recorded. On the only other patch reef inhabited by *S. partitus*, a single individual from the species existed alongside one *S. diencaeus* and six *S. leucostictus*. The remaining three reefs in the study, where *S. partitus* was not present, were all occupied by *S. leucostictus*. One of the three was exclusively occupied by *S. leucostictus*, one by both *S. leucostictus* and *S. diencaeus,* and one by *S. leucostictus, S. diencaeus and S. adustus;* this being the only location where *S. adustus* was identified during this study.

The two variables that showed the most significant interspecific differences amongst *Stegastes spp.* following the use of one-way ANOVA tests were the number of *Haemulidae spp.* within 1 m of an individual's territory and the total number of *Haemulidae spp.* across the whole patch reef (ANOVA: $F_{2,27} = 9.00$, $p<0.01$). Both *S. diencaeus* and *S. leucostictus* living alongside much larger numbers of *Haemulidae spp.* than *S. Partitus*, both in the vicinity of an individual's territory and across the whole reef. *S. diencaeus* was found consistently amongst large populations of *Haemulidae spp.*, whereas *S. leucostictus* could be found in amongst large schools or entirely isolated (Figure 2.3, Table 5.1, Table 5.2). The next two variables that showed the greatest significant difference between species were the height of each individual in relation to the height of the reef (ANOVA: $F_{2,27} = 6.00$, $p<0.01$), followed by its height from the sea floor (ANOVA: $F_{2,27} = 5.98$, $p<0.01$). *S. diencaeus* was normally furthest from the sea floor, where as *S. Partitus* was the species found closest to the top of the reefs that it occupied. Notably, the results for *S. diencaeus* and *S. Partitus* were reasonably similar, but *S. leucostictus* had much lower values for both variables (Figure 2.3, Table 5.1, Table 5.2). Other factors that had a significant p-value included the widest perpendicular width of each individual's territory (ANOVA: $F_{2,25} = 4.67$, $p<0.05$), and the height of the reef from the sea bed (ANOVA: $F_{2,27} = 4.62$, $p<0.05$). Closely linked in with the height of the individual, *S. diencaeus* occupied the highest reefs, as well as having the widest territories. *S. Partitus* was next in line for both height and width, with *S. leucostictus* occupying the smallest reefs and having he smallest territories (Figure 2.3, Table 5.1, Table 5.2).

Not all of the variables taken proved to have significant variation between species however, with ANOVA suggesting that there was no significant variation between species for widest width of each territory (ANOVA: $F_{2,25} = 2.57$, $p>0.05$), the number of holes (ANOVA: $F_{2,27} = 0.65$, $p>0.05$) and the mean size of holes within a territory (ANOVA: $F_{2,27} = 0.28$, $p>0.05$). As

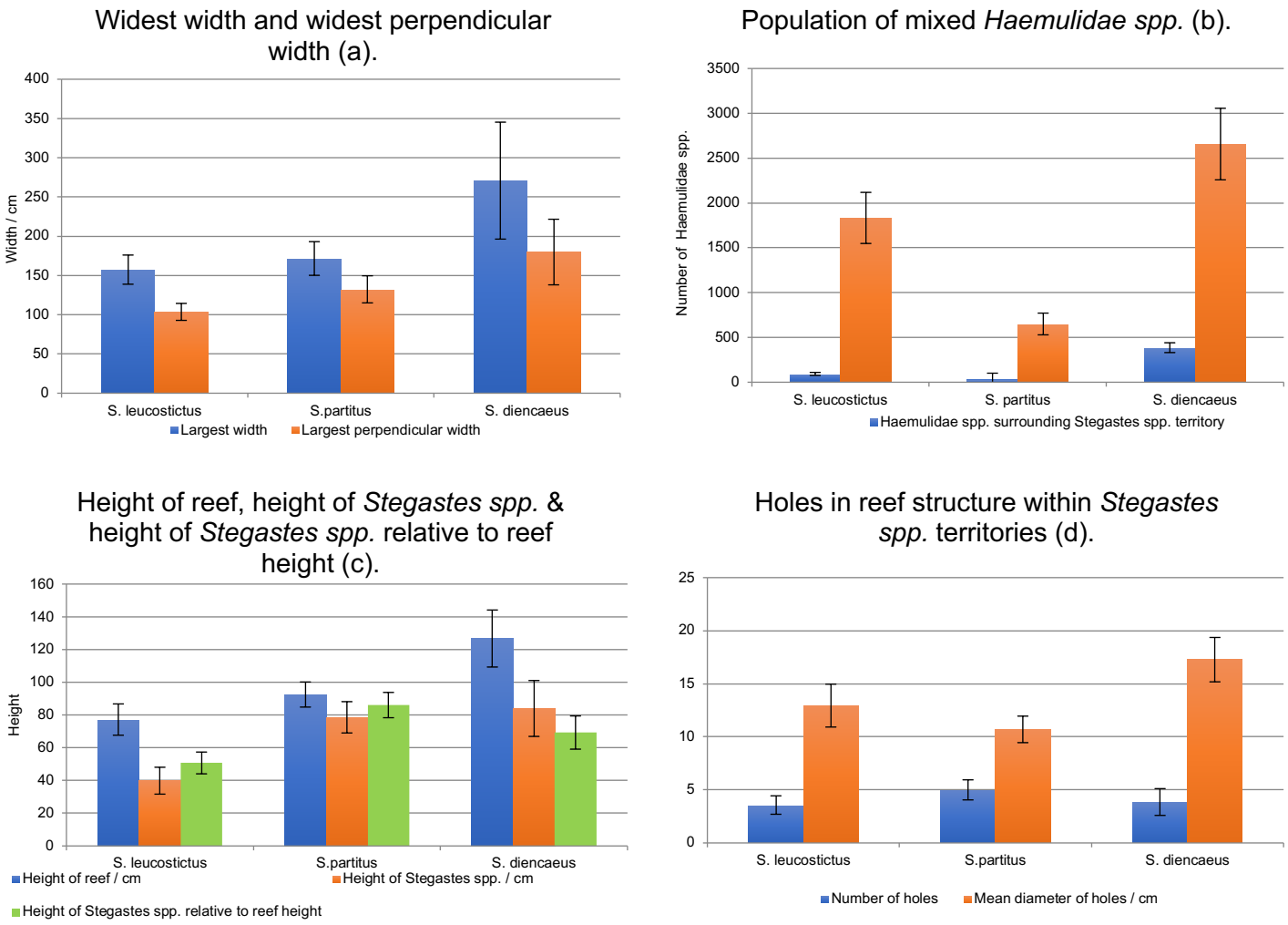

Figure 2.3. Supporting data comparing means of variable between species. (a) Comparing the two largest perpendicular widths of each species territory. (b)Comparing the number of Haemulidae spp. surrounding the reefs and territories occupied by each Stegastes spp. (c) Number and size of holes in substrata within each Stegastes territory. (d) Variation in height of Stegastes, height of reef and height of the Stegastes relative to the reef (out of 100).

one width showed a significant difference between species and one did not, it is difficult to draw a conclusive result from this. The same hierarchy, however, existed in both results with *S. diencaeus* having the widest territories, followed by *S. Partitus* and lastly *S. leucostictus.* Having a similar number and size of holes is a less surprising result, with all species being of a similar size, the data had very similar average hole sizes and numbers of holes found within all territories (Figure 2.3, Table 5.1, Table 5.2).

In addition to the differences detected using ANOVA, Multi Factor Analysis (MFA) was also conducted to ascertain how interactions between variables influenced the whole data set. The variation explained by the primary MFA factor (F1) was 38.64%, with the secondary factor (F2) explaining a further 21.36% (*Figure 2.4*, Table 5.3). When species were visualised in F1/F2 space, the majority of *S. diencaeus* were clustered together with strongly positive F1 and positive F2 values, scoring the highest mean F2 value as well as the highest individual F1 and F2 values. *S. leucostictus* were generally clustered with low or negative F1 values, alongside *S. partitus,* with the latter tending to have marginally higher F1 values and the former slightly larger F2 values. The data for the two species has many overlapping points, as seen in Fig 2.3, but this is due to co-varying factors – different factors that had similar influences on the F1 & F2 axes. This is where the mean values become key to show the separation between the two species.

The dominant variables driving F1 values were both the widest width and the widest perpendicular width of each individual's territory, the height of the reef, the height of the *Stegastes spp.* individual from the sea bed, and the number of Haemulidae *spp.* surrounding a *Stegastes* territory. As the ANOVA tests found no significant difference on the widest width, it is likely this variable had a similar influence across all test species. The heavy influence of the width and the height based variables will have skewed *S. diencaeus* to give the species its highly positive F1 score as well as separating *S. partitus* from *S. leucostictus* . The F2 values were predominantly influenced by depth, average hole size in the substrata of an individual's territory and the number of Haemulidae *spp.* around the territory as well as across the whole patch. The variables based on *Haemulidae spp.* will have provided the positive skew on the F2 axes, separating *S. partitus* from *S. leucostictus* and *S. diencaeus.* The number of holes in a territory had the least effect on either the F1 or the F2 axes, which links in closely with the results seen in the ANOVA tests.

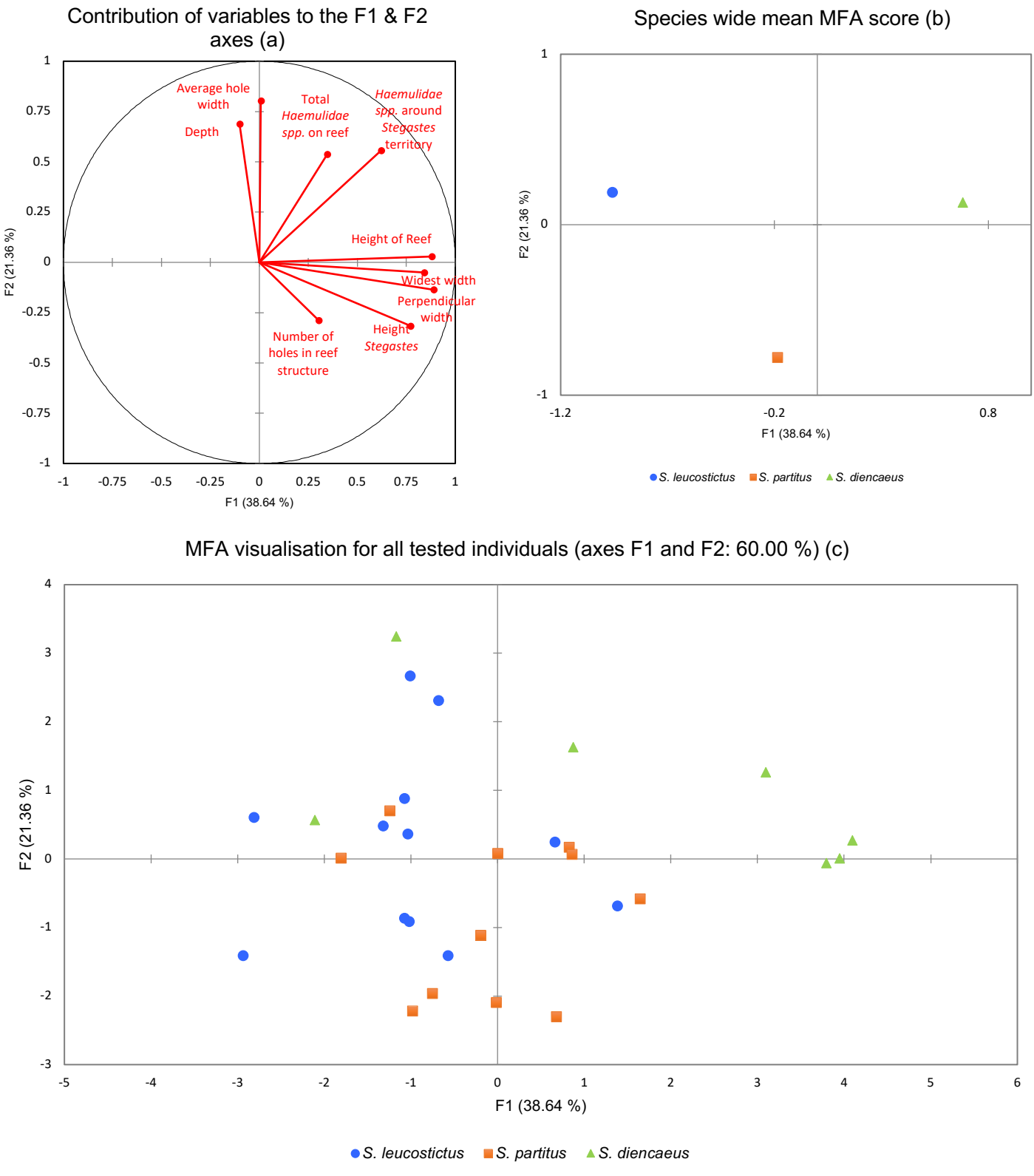

Figure 2.4. Influence of environmental parameters on distributions of Stegastes spp. (a) Contribution of variables to Multi Factor Analysis (MFA). (b) Mean MFA score for each Stegastes spp. (c) Visualised results of Multi Factor Analysis from F1 and F2 variation. Eigenvectors and factor loadings can be found in table 5.3.

2.3.1 Incomplete data

As previously mentioned, *S. adustus* was discounted from analysis due to rarity (only two observations). Three further individuals were discounted from use in the MFA as they had incomplete environmental data. These individuals, two results for *S. leucostictus* and one result for *S. partitus,* were still used where the data were sufficient for one-way ANOVA.

2.4 Discussion

The results of the One-way ANOVA and MFA tests detect clear separation in the niches occupied by each species, driven at least in part by the environmental variables considered, which has led to several key findings including a clear hierarchy amongst species.

Where *S. diencaeus* is clearly in its own niche in the MFA results, both *S. partitus* and *S. leucostictus* had many overlapping F1/F2 data points in the MFA. The mean values for each species, however, clearly showed a split. The differences in the niches *S. partitus* and *S. leucostictus* occupy were the height above the sea bed, an individual's height relative to that of the patch reef and the number of *Haemulidae spp*. across the patch reef. The marginally larger value for *S. partitus* on the F1 value was due to the substantial difference in height occupied on the reef, with the species uniformly occupying the territories around the top of the reef, while *S. leucostictus* was found lower down. *S. diencaeus,* like *S. partitus*, occupied territories near the top of the reefs, in particular tending to occupy patches which were much taller than others in the area. This contributed to the high F1 values scored by many of the *S. diencaeus* and is the first indication of this species' dominance amongst the *Stegastes spp.* in the Cape of Eleuthera. Occupying the top of the tallest patch reefs provides an advantageous position (Harborne et al., 2011), and is key finding of this study as it is one of the variables that determined the hierarchy of species surveyed. As both *S. diencaeus* and *S. partitus* occupy these physically ideal territories, it appears that *S. leucostictus* is out-competed from these locations, then forming its own niche lower down on patch reefs. This sacrifice in height,

however, allows it to occupy the optimal reefs, invariably inhabiting patch reefs alongside *S. diencaeus* individuals that were near or on the highest points of the patch. This suggests that *S. partitus* occupies territories where *S. diencaeus* is not present as these two species were only once found co-existing on a single patch reef. The outcompeted *S. partitus* locates alternative reefs on which to settle, sacrificing the optimal reef communities to be able to swim higher up on the patches it does occupy to gain the advantageous high position of the reef.

Haemulidae spp. were a key contributor to the variation on both axes, but more so on the F2 axes. Where *S. leucostictus* was not competing against the other *Stegastes spp.* at the top of the reef, they were able to inhabit a separate niche living lower down on amongst the schools of *Haemulidae spp*. *S. leucostictus* territories would be surrounded with 0 to 500 *Haemulidae spp.* within 1 m of their territory. Although the species do not occupy the advantageous heights of the reef, perhaps it could be considered that the species have received an alternate benefit in the form of greater protection from predation. Being smaller than the *Haemulidae spp.* and of a similar colour will make *S. leucostictus* difficult to distinguish for passing predators of the species or it's eggs. For *S. diencaeus* individuals, there was similarly large numbers of *Haemulidae spp.* immediately surrounding their territory. All but one of the individuals surveyed from the species had 300 or more Haemulidae spp. within 1 m of their territory, however, there is an abstract disparity between these results for *S. diencaeus* and *S. leucostictus.* Unlike *S. leucostictus, S. diencaeus* was not swallowed by the schools of *Haemulidae spp.* surrounding its territory, using the high up position that the species so often occupied on a reef to allow it to sit above the schools only occasionally diving amongst them to chase them away or to hide from potential threats. This once again supports the key finding of this study that the optimal reefs for *Stegastes spp.* are those that were occupied by *S. diencaeus* and *S. leucostictus* alongside the schools of *Haemulidae spp.* In contrast, all but one *S. partitus* territory had less than 50 *Haemulidae spp.* in the immediate vicinity of their territory, with the majority having none. Although this will reduce threat by allowing for a greater

field of view for *S. partitus*, the fact that the species was mostly secluded from the other *Stegastes spp.* and missed the highest reefs supports the hierarchy suggested here.

A similar pattern of *Haemulidae spp.* distributions was seen across the entire patch reef, with *S. diencaeus* living exclusively on high population reefs (2,200-3,000 individuals of *Haemulidae spp.*), *S. leucostictus* occupying territories with up to 3,000 *Haemulidae spp.*, while 8 of the 12 *S. partitus* occupied reefs with small populations of *Haemulidae spp.* (<150 individuals). As the majority of *S. leucostictus* choose to inhabit reefs alongside *S. diencaeus, as well as* a larger number of *Haemulidae spp.,* this could be an indicator of a healthy location in which to settle. This furthers the hypothesis that *S. diencaeus* is competitively excluding *S. partitus*. The outcome of this competition is that the presence of *S. diencaeus* and *S. leucostictus* may promote settlement of *Haemulidae spp.,* enhancing the nursery and possibly leading to further recruitment, enhancing reef health. The deduction that these *Stegastes spp.* are promoting *Haemulidae spp.* settlement developed as *Stegastes spp.* will be static occupying a territory, whilst the *Haemulidae spp.* are passing through the reefs as a part of their nursery habitat on the way to fore reefs. It should be considered though that any settling *Stegastes spp.* may be influenced by the presence, or lack of in the case of S. Partitus, *Haemulidae spp.* of The patch reefs in this nursery are vital to *Haemulidae spp*. settlement as they provide protection from predators (Pereira & Ferreira, 2013). Settling in larger numbers provides the greater protection of schooling and health benefits (Yeager et al., 2014). The protection of a healthy reef and schooling encourages the *Haemulidae* spp. to slow their swimming speed and gravitate towards the bottom of the reef, away from the advantageous heights of the top of the patch reef (Pereira & Ferreira, 2013). The evidence from these papers was seen around many patch reefs in the Cape of Eleuthera. *S. leucostictus* was able to tolerate *Haemulidae spp.* swimming through its territory, to avoid competition for territory against *S. diencaeus* and *S. partitus*. *S. diencaeus* would also inhabit patch reefs alongside the *Haemulidae spp.,* utilising the territories it has competitively excluded the other *Stegastes spp.* from to swim above the low and slow moving *Haemulidae spp.* schools. This leaves *S.*

partitus inhabiting less populous reefs, but still able to tolerate low numbers of *Haemulidae spp.* on the patch, but only away from the vicinity of its territory.

There is further evidence of interspecific variation amongst *Stegastes spp.* when considering the size of the territory that each species occupies. The largest width was measured followed by the largest width perpendicular to it, to give a reflection of the size of the area occupied by each fish. Each variable made a substantial contribution to the F1 axes in the MFA (Widest width F1 = 0.451, Widest perpendicular width F1 = 0.477). However, only the perpendicular width proved to have a significant difference between species (Widest width ANOVA: $F_{2,28}$ = 2.57, $p>0.05$; Perpendicular width ANOVA: $F_{2,59}$ = 4.67, $p<0.05$). This suggests that there was some limited variability in territory occupation between species. *S. diencaeus* occupied both the biggest territories as well as the greatest heights on the reef, further supporting the hypothesis that *S. diencaeus* is the dominant species of the three, as well as explaining why *S. partitus* may struggle to co-exist. By occupying a smaller territory size lower down the reef, *S. leucostictus* avoids niche overlap with *S. diencaeus.*

Not all variables did prove to be a niche between the surveyed *Stegastes spp.* The complexity of the substrata is a physical characteristic of reefs that would encourage settlement of *Stegastes*, amongst other reef fish species, due to the advantage it affords over predators and conspecific species (Wilson et al., 2010; Harborne et al., 2011). Two variables that reflect the complexity of the substrate – number and mean size of holes in the substrata within a territory – showed no significant difference between species in ANOVA tests. The average hole size was the largest contributor of all the variables to the F2 axes in the MFA (F2 = 0.579), whereas number of holes did not contribute substantially to either axes (F1 = 0.162, F2 = -0.208). This suggests that although the number of holes may not be of importance, the size of the holes is, however it is of equal importance to all three of the species studied. Thus, there appears to be a collective requirement amongst all of the surveyed species, in line with the referenced previous studies, to have some holes in the substrata of a certain size. The final variable,

depth, also showed no significant difference between the species with ANOVA, but was a major contributor to the F2 axes in the MFA (F2 = 0.497). The consistency in results across the species surveyed, which resulted in the strong F2 contribution, was due to the survey being conducted on what is effectively a sunken plateau at the same point in the tidal cycle.

2.4.1 Limitations

This study was only able to collate data from a limited number of reefs, therefore a small number of *Stegastes spp,* in the time period available. Surveying a larger number of reefs would have given a larger dataset which would have provided results with increased statistical power and reliability. A larger study, however, would take longer and pose the challenge in avoiding variation in season, tide, weather and the lunar cycle. The survey would also have to consider other factors such as how boat traffic may manipulate results. This study was further limited by the number of variables not covered. This includes intrapopulation characteristics of individual damselfish (sex, presence of eggs, guarding behaviour), abiotic variables (rugosity, flow rate), and the presence of other species in and surrounding the territory (conspecific species, algae, coral, distance from mangroves). This limitation also includes that each individual site was not pitted against the others for statistical analysis as any numerical representation of location would have severely manipulated the results of the MFA, giving bias to certain reefs over others whether they were randomly numbered or scored my latitude and longitude.

2.4.2 Further study

This study could be furthered by the consideration of an increased number of variables, including further abiotic variables such as rugosity, flow rate, and surrounding benthic composition. This would maintain the simplicity of gathering data while potentially providing further insight into the purely physical habitat choice of *Stegastes spp*. However, priority for further study should primarily be given to identifying the species present in the immediate territory of the damselfish and those that make up the surrounding community; including

invertebrate, coral and algae species. There are a wide range of interactions experienced by other species with *Stegastes spp.* and perhaps this may influence their settlement. This is of interest given the findings of this study's one biotic interaction, that of *Stegastes spp.* and Haemulidae *spp.* Aside from the interactions, an overarching reef population study may indicate reef health which could be influencing *Stegastes spp.* territory selection. Further to this, a future study could be conducted in areas of increased variation to provide further contrast to the data collected at Cape Eleuthera. For example, surveys could consider reefs that have Haemulidae *spp.* but no *Stegastes spp.,* patches that host neither of these species, or, on a more detailed scale, could survey patch reefs which both species inhabit, split into areas they co-occupy and areas they do not. The study could be continued on to other types of reefs as well, for example on fore reefs, as *Stegastes spp.* may be present in larger populations on other types of reefs (Harding et al., 2006). The method may need to be adapted for the use of transect surveys to achieve this. The findings of this study could also be specifically built on by a future study looking to identify whether the schools of *Haemulidae spp.* are offering protection by making Stegastes spp. indistinguishable to predators.

Given the influence of coral reef sounds in guiding settling *Pomacentridae* larvae to settle after their pelagic life phase (Simpson et al., 2005), acoustic recordings to identify characteristics of the soundscape that attract this family could be used to see if there are any underlying sounds that cause variation in interspecific attraction. This would offer a real insight into the relationship between *Stegastes spp.* settlement and Haemulidae *spp*. A choice chamber study (e.g. Simpson et al., 2010) could be used with *Stegastes spp.* and Haemulidae *spp.* to identify which species influence the settlement behaviour of the other. Both species would be given the opportunity to settle with or without the other species present. This could be done very simply in a wet lab by playing the sounds of one species to the other from one side and ambient reef noise or no noise as the other choice. With the results from this, more complex and increasingly detailed choices could be tested.

2.4.3 Summary

This study has explored an array of biotic and abiotic factors relating to the territories occupied by *Stegastes spp.* in the Cape of Eleuthera, which has led to the development of three key findings. The first is the equal importance of holes in the substrate which all *Stegastes spp.* select for their territory, offering them transit away from larger bodied predators. The second key finding is the clear hierarchy shown by *Stegastes spp.* in the patch reef system of Cape Eleuthera. *S. diencaeus* controls the highest reefs, as well as those that appear to be the healthiest with the large schools of *Haemulidae spp.* Simultaneously *S. diencaeus* is competitively excluding *S. leucostictus* form the heights and *S. Partitus* from the optimal reefs. *S. Partitus* then excludes *S. leucostictus* from its locations, but *S. leucostictus* often seems to have formed a niche living for itself, utilising the schools of Haemulidae spp. for protection or occupying reefs without other *Stegastes spp*. The third and final key finding is the relationship between *Stegastes spp.* and *Haemulidae spp.* and how this may provide a potential valuable indication of reef health. The relationships highlighted here provide an interesting insight as to the importance of a variety of biotic and abiotic factors to settlement behaviour and hierarchical niche fragmentation within *Stegastes* genus.

3. Impacts of chronic boat traffic on coral reef populations in The Bahamas

Caribbean coral reefs, as with others around the world, are suffering from an increasing predicament of threats including the building threat from anthropogenic noise. The waters encapsulated by the Cape of Eleuthera hold a system of more than 200 patch reefs which act as an intermediate nursery ground for species using the mangroves, as well as a home to a large community of other species. This study set out to identify if boat traffic had an effect on the communities of a variety of patch reefs. Three pairs of patch reefs off the coast of Eleuthera, the Bahamas, were either treated with boat traffic or protected from it. Species richness and density improved across protected reefs, with trafficked reefs showing a reduced rate of improvement or a decline. However, reefs that had previous long-term exposure and were in areas of higher traffic did not improve even when protected. Protecting these reefs from boat traffic also has a notable effect on recruitment of *Haemulidae spp.* The most significant change was the presence of *Haemulidae spp.* that chose to settle in large numbers on reefs with limited passing boat traffic, whilst far fewer settled in areas with more regular boat traffic. This outcome provides an interesting insight into the effect of anthropogenic noise on coral reef communities and will be of use in planning for future studies as well as protection.

3.1 Introduction

Anthropogenic noise poses a range of threats to the marine environment, with many of the sources coming from shipping (Slabbekoorn et al., 2010). From small boats to large tankers, each contribute to the marine soundscape with engine noise, hulls slap and, in some cases, SONAR. There is still a limited amount of research into the effects of anthropogenic noise in the marine environment but much of it has focused on how individual species are affected as well as the production and modelling of noise (Popper & Hastings, 2009; Radford et al., 2014). There has been limited research looking at the effect of traffic manipulation on a whole community.

Coral reefs provide a habitat for many species, with patch reefs acting as an important intermediate stage for individuals transferring from the nurseries provided by seagrass beds and mangroves (Williams et al., 2017; Nagelkerken et al., 2002). A reef's acoustics are recognised as playing an important part in recruitment and cause both positive and negative taxis (McCauley et al.,2000; Radford et al., 2011; Simpson et al., 2011; Huijbers et al., 2012; Lillis et al., 2016). Sources of anthropogenic noise are known to influence an individual's selection, which can lead to poor habitat choice (Holles et al., 2013). This makes small yet diverse patch reefs ideal to study the influence of anthropogenic noise at community level.

Studies have tracked larger ships in many environments and monitored their effect on the marine creatures in their environments (Castellote et al., 2012; Merchant et al., 2014; Williams et al, 2014). There has also been some work with smaller vessels, which are easier to manipulate (Codarin et al.,2009; Picciulin et al., 2010; Rako et al., 2013). These studies, like most others, focus on a limited number of species or the boat noise itself and not the wider impact on the ecosystem.

The aim of this study was to trial a study method which considered the effects of anthropogenic noise on a population rather than an individual species. This is unlike work previously conducted and intended to achieve the feasibility of the study. The null hypothesis was that there would be no significant change between the reefs experiencing an increase in traffic to those protected from anthropogenic noise.

3.2 Material & methods

3.2.1 The study site

The study was conducted between March 2015 and June 2015 off the coast of Eleuthera, the Bahamas (N 24º50'05", W 76º20'32"). The waters encapsulated by the Cape of Eleuthera contain a system of in excess of 200 patch reefs. Water depth at the sites used by this study varied between 1.9 m and 3 m.

Site selection was based on the initial conditions imposed (*Figure 3.1; Table 3.1)*. Using the physical data collected form 230 patch reefs, three groups were created each consisting of 10 reefs with similar abiotic characteristics (width, perpendicular width, height, depth and rugosity based on average chain length). The primary focus for the selection of patch reefs was the two perpendicular widths of the reef, as this would present a theoretical area by which it would be possible to compare patches on their assumed size. These groups were then scrutinised to identify reefs which shared further similarities (flow rate, benthic habitat and location). For this narrowing of the selection, the location was of particular importance to ensure that previous exposure to boat traffic was similar within the pairs. From the remaining selection, pairs of reefs were randomly selected. Each reef had its boat traffic from the past year checked using GARMIN HomePort (*Table 3.2*), ensuring that boat traffic passing within 250 m was similar. Within each pair of reefs (*Table 3.1)*, one would be subject to an increase in the level of boat traffic passing within 250 m of the patch whilst the other would be protected with a decrease in traffic. The three pairs all had slightly varied features to determine how increased

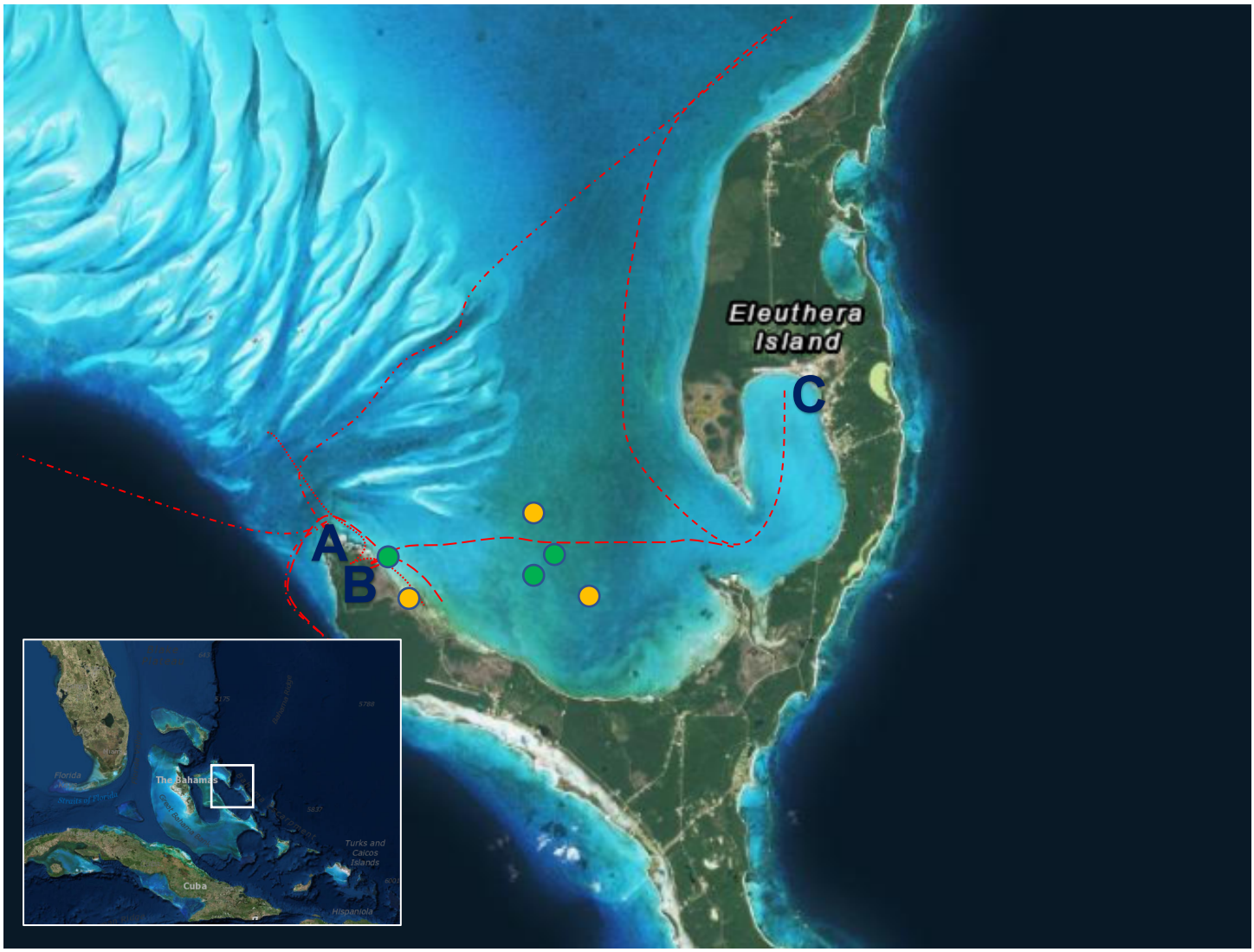

Figure 3.1. Cape of Eleuthera: study site in detail. (captured from regional image in bottom left hand corner). Blue letters are sources of boat traffic; (A) Cape Eleuthera Marina, mostly private yachts and sports fishing vessels; (B) Cape Eleuthera Institute boathouse cut; vessels listed in Table 3.3 as well as small fishing craft; (C) Rock Sound dock, regular small cargo vessel and some private vessels. Green dots from left to right: EW35, Howard, Tarran. Orange dots from left to right: Ofra, EW57, Hammerhead. Red lines track regular routes taken by boat traffic; (dots) local fisherman; (dashes & dots) private boat traffic; (short dash) commercial and private traffic; (long dash) research vessels).

or decreased boat traffic would affect a wider range of habitats, and their communities (*Table 5.4)*.

The first pair of reefs, named EW35 and Ofra, were characterized by being the smallest in

Table 3.1. Abiotic characteristics of surveyed patch reefs.

Reef name	Height of Reef / m	Depth / m	Widest width / m	Perpendicular width / m	Theoretical area/ m^2	Average chain length / cm
35	0.78	2.85	2.80	1.90	5.32	74.00
Ofra	0.80	1.90	2.37	2.12	5.02	87.00
Tarran	0.60	3.00	3.30	2.45	8.09	73.59
57	0.68	2.90	3.20	2.30	7.36	79.85
Howard	1.30	2.60	7.63	6.30	48.07	79.33
Hammerhead	1.47	2.90	10.50	5.10	53.55	71.98

Table 3.2. Treatment and boat traffic history of surveyed patch reefs. Each reef is identified whether it was the traffic or avoid reef within its pair. Boat traffic in the run up to the study is identified over the course of 1year, 6 months and three months. Boat traffic during the study is spilt between the total number of passes recorded and the number not including surveys as the approach to the reef was controlled in these instances.

Reef name	Traffic or avoid?	Boat traffic passing reefs prior to this study			Boat traffic passing reefs during the period of this study (4 months)	
		1 year	6 months	3 months	Total number of boat passes	Number of boat passes not including surveys
35	Traffic	20	20	19	60	55
Ofra	Avoid	17	16	15	23	16
Tarran	Traffic	6	6	2	26	19
57	Avoid	3	3	3	10	2
Howard	Traffic	6	3	0	33	28
Hammerhead	Avoid	5	3	3	15	6

Figure 3.2. Tidal flow around the Cape of Eleuthera. Purple arrows represent high tidal flow areas.

size (*Table 3.1*). Two variables that made these reefs distinct from the other patch reefs were the high tidal flow rate (*Figure 3.*2) and the already elevated level of traffic in the area from both the research facility and the local fishermen. The high tidal flow rate was caused by a canalization of incoming and retreating tides by a large sand bank. This posed difficulties anchoring and surveying at both sites and likely influenced the species able to survive on reefs in the area. Both patch reefs had populations consisting of unusually high levels of juvenile fish, with a low individual biomass across all the species present. To survive in this area is an unattractive prospect with a lot of energy being expended swimming against the tide and through startle response to boat traffic. Although they were located near the mouth of a mangrove, neither has a population of juvenile *Haemulidae spp.* that is common in the area.

Equally, where many patches consist of more than one large structure with smaller patches surrounding the reefs, both of these were individual growths away from any other substantial benthic habitat. The variations in the physical stature of these reefs and there surrounding benthic habitat was likely, once again, down to the flow rate.

EW57 and Tarran, the second pair, were marginally larger than the first pair but were protected from the powerful tides due to being located away from the ingress and egress of the tide. The pair were just over 7 km out into the waters of the Cape of Eleuthera. This meant that there was minimal traffic passing either patch reef making it easier to monitor and control as only research station boats tended to travel through this area, and even this traffic was infrequent. Like the previous reefs, there was unusually low numbers of juvenile *Haemulidae spp.* Both reefs had sparse sea grass in the surrounding benthic habitat.

The final pair of patch reefs, Howard and Hammerhead, were two of the largest patches in the Cape of Eleuthera. This pair shared very little in common with the first pair of patches but a small amount with the second amount due to location, which once again was sheltered resulting in low tidal flow rates. Unlike the previous pairs, these patches were substantially larger in size as well as having a cluster of surrounding smaller substrata, fire corals and patches of sea grass. The community had much higher species richness and biomass, with both reefs incorporating the presence of large schools of a variety of species and were prone to visits from more mobile species.

3.2.2 Boat traffic & GPS recordings

Traffic within the area was manipulated in order to minimize passes of the “avoid” reefs while increasing traffic at the “traffic” patches. With the exception of the research vessels (*Table 3.*3) and fishermen in the vicinity (*Figure 3.3*), the shallow nature of the area in which the patch reefs are located minimizes any other traffic. Almost without exception during the period of the

Table 3.3. Vessels from the Cape of Eleuthera Institute.

Name	Boat type	Length / ft	Weight / lbs	Engine Size	Prop Size / "	Hull type
Anita Smiles	Carolina Skiff	24	1000	115HP OB	14	Flat
Bonita	Carolina Skiff	20	900	60HP OB	10	Flat
Dave & Di	Panga	26	2500	160HP	14	V
Kenny T	Panga	26	2500	160HP	14	V
Mac Daddy	Panga	26	2500	160HP	14	V
Mary Alice	Panga	26	2500	160HP	14	V
Red Rising	Panga	26	2500	160HP	14	V
Simon Says	Key West	24	3000	300HP	15	V
Scute	Eduardono Skiff	17	700	40HP OB	10	V

study, other vessels would hug the coast to the east following the channel into Rock Sound or would stick to the north and west to approach the marina on the northern tip of the Cape of Eleuthera (*Figure 3.1*). Therefore, the heaviest source of boat traffic in the locality of the test sites was that from the Cape Eleuthera Institute (CEI). The research conducted at the Institute occurs at a variety of locations throughout the patch reef system, as well as at other sites that require travel through or near to the patch reefs monitored in this study.

Figure 3.3. The vessels used by the local fisherman in the boathouse cut of the Cape of Eleuthera Institute.

To reduce incursions of the “avoid” reefs and increase traffic on the “traffic” reefs, buoys were located near to patches to identify whether they should be avoided (orange) or trafficked (green). Colour selection may appear to be trivial, but a vivid

orange stands out in the sea no matter the weather, whereas a green buoy is not as easily visible at all times. It was deemed more important to protect the “avoid” reefs than ensure that all boats passed the traffic reefs at all times. GPS co-ordinates were entered on all of the boats with GARMIN GPSmap 441s using GARMIN HomePort software as an additional precaution. The combination of GPS marking, tracking and support software allowed for tracking of traffic before and during the study for the Panga vessels that had the Garmin GPS system fitted. As this was the majority of the vessels, this gave an accurate reflection of the traffic from CEI (*Table 3.3).* Other boats from the research station that were navigating by handheld GPS were requested to record when they past any reefs. The only other traffic that would still pass by that could not be controlled were the small craft of a few local fishermen that would leave out of the same cut as the CEI dock. These vessels were small in hull and engine size, only travelled at low speeds, but would still offer semi regular traffic; fishermen would visit differing sites, taking varying routes, departing 2-3 times a week. However, as they only tend to travel across the already heavily trafficked Ofra and EW35 reefs, their impact should be minimal.

Passes of a reef were classed as any intrusion within 250 m. Where possible, boat speed was noted down alongside the date and time for a pass on any reef. Surveys required encroachment within the 250 m perimeters surrounding each reef, but disturbance was minimized by reducing boat speed on approach to below 10 knots or so that the engine was operating at less than 1200 RPM. Prior to entering the cordon, the flow of the water would be determined. This meant that upon breaking the 250 m barrier, the research vessels could be placed up flow of the reef, and the engine set to idle to further reduce the influence of the boat. The anchor would then be dropped so that the boat would be able to gently float down-tide stopping near to the reef. Once the anchor was set, normally leaving the boat approximately 50 m from the reef, the engine would be cut, and a soak period would allow any disturbance to return to normal. This method of approach was used regardless of whether the reef was a “traffic” or “avoid” reef to ensure parity for surveys.

3.2.3 *Surveys*

Where possible surveys were conducted in sets, linked as close together in time as possible, to help eliminate variables from the lunar phase as well as the weather. This meant that 38 of 48 surveys were conducted within 48 hours of their partner reef, 30 of these were conducted on the same day so the time between surveys will have been the time taken to move between sites. After arriving at each reef, surveyors would enter the water and document species within and up to 5 m around the reef. A maximum time of 20 minutes was set for any survey, but this was never exceeded. All surveyors were free diving, as the shallow water enabled a full survey to be conducted without the additional noise and disturbance that can be incidental with the use of diving equipment. A total 53 species were identified during this study, many of which were present in various life stages.

3.2.4 Statistical analysis

These data form a total of 48 surveys, eight per site, were input into a database (ACCDB Database pro). XLStat software was used to conduct Multi Factor Analysis (MFA) to determine the relative importance of each variable on a reef's population. The variables included both abiotic and biotic variables as this would provide a more accurate reflection of the community and its habitat. ANOVA tests were also used to look at individual relationships using Statplus.

3.3 Results

Multi variant statistical analysis, data for which is found in *table 5.5*, made it possible to elucidate that there was a clear separation within paired sites experiencing an increase in traffic and those patch reef experiencing reduced boat traffic (*Figure 3.4*). The variables that were the largest contributors to the F1 factor loadings (50.39%) were the species present, and the two largest perpendicular widths. The F1 axes, therefore, gives the best indication of how the treatment affected the community living on each reef. The significant variables for F2 values (14.38%) were the depth and average chain length. As both of these remained

consistent throughout, it means that the variables that cause F2 deviation will have smaller values for factor loadings than expected. Due to this, F2 variation will be caused by some of the species present and the number of boat passes each reef was exposed to. The overall variation captured for the combined F1 and F2 axes in the MFA was 64.78%.

The four smallest reefs all had negative F2 values for each survey, whereas the larger pair of reefs both had positive values throughout. Each pair of reefs, owing to their unique qualities, displayed slight differences over time. Two pairs of the patch reefs were separated from the reef that they were paired to that was experiencing the opposite treatment by F2 values. The two reefs with positive F1 values showed an inverse relationship with F2 values, compared to that of their counterparts undergoing the same treatment on the smaller patches. For example, where the large reef protected from boat traffic, Hammerhead, had a positive F1 value as well as a more positive F2 value than the other large reef that was being trafficked, Howard, the opposite was true for the small reefs with reduced traffic. These had negative F1 values as well as lower F2 values than the reef they were paired to experiencing extra boat traffic. All of these smaller patch reefs also had more consistent results to those of the larger reefs, suggesting that the larger populations had more variable populations and were more prone to flux.

The F1 values over time are a reflection of how a reef's population is coping with the treatment it is exposed to. This is due to the major contributors to the F1 factor loadings being the fish species surveyed and the width measurements; where the latter did not change between surveys, the former was the only variable to change over time. The smallest pair of reefs, which were already heavily trafficked prior to the study, showed similar levels of change between the first and last surveys (EW35 F1 = -0.251; Ofra F1 = -0.258). The other pair of small reefs showed differing results with the reef with increased traffic exhibiting a decrease in F1 value while the reef with reduced traffic levels showed a distinct increase (Tarran F1 = -0.096; EW57 F1 = 1.325). The larger reefs both showed an increase in F1, but the undisturbed

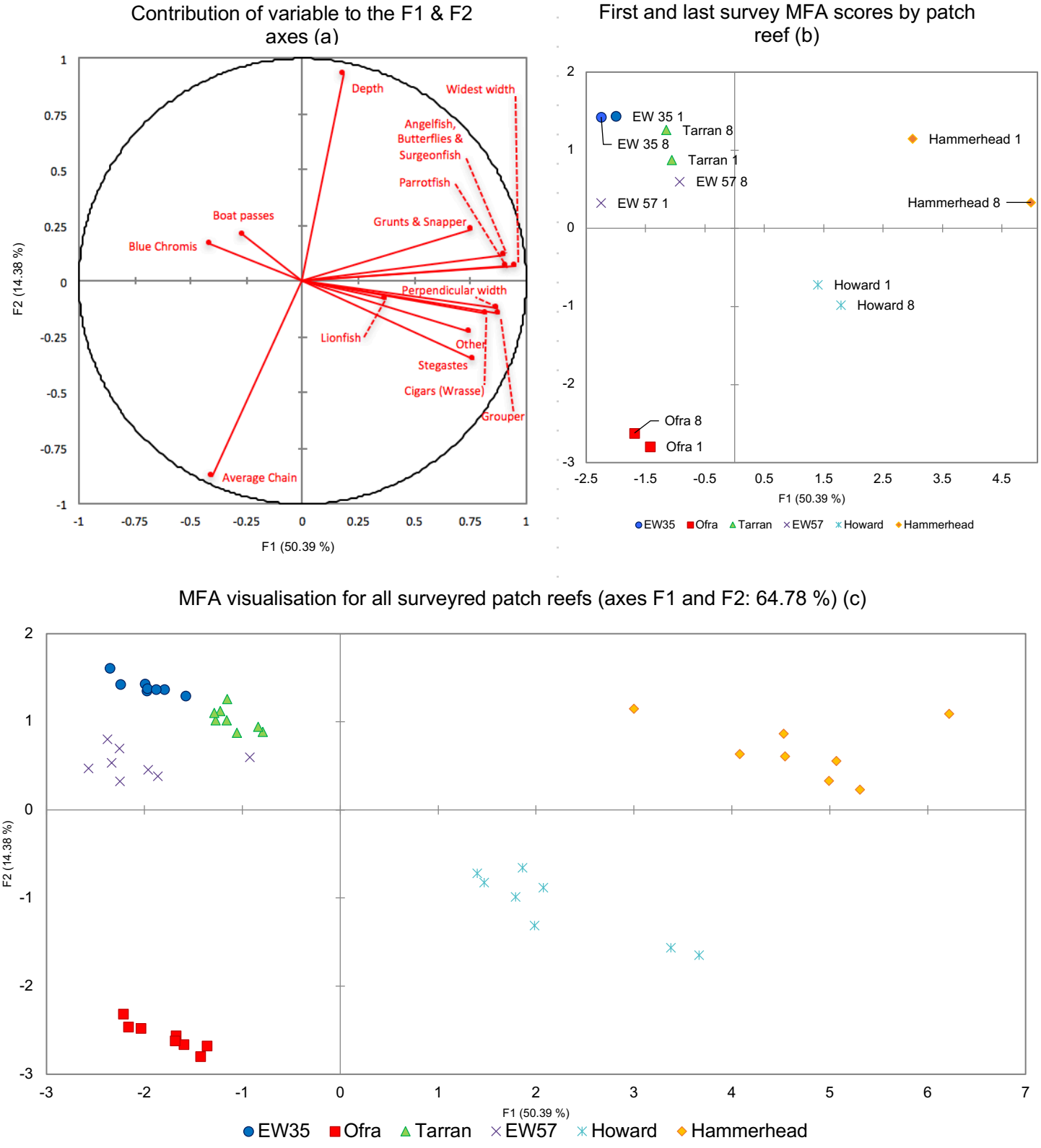

Figure 3.4. Multi Factor Analysis results for the effect of chronic noise on fish populations, inclusive of abiotic variables. (a) Contribution of each of the variables to the F1 and F2 axes. (b) MFA results from the first and last survey of each reef. (c) Full MFA results for all surveys on all patch reefs. Eigenvectors and factor loadings can be found in table 5.6.

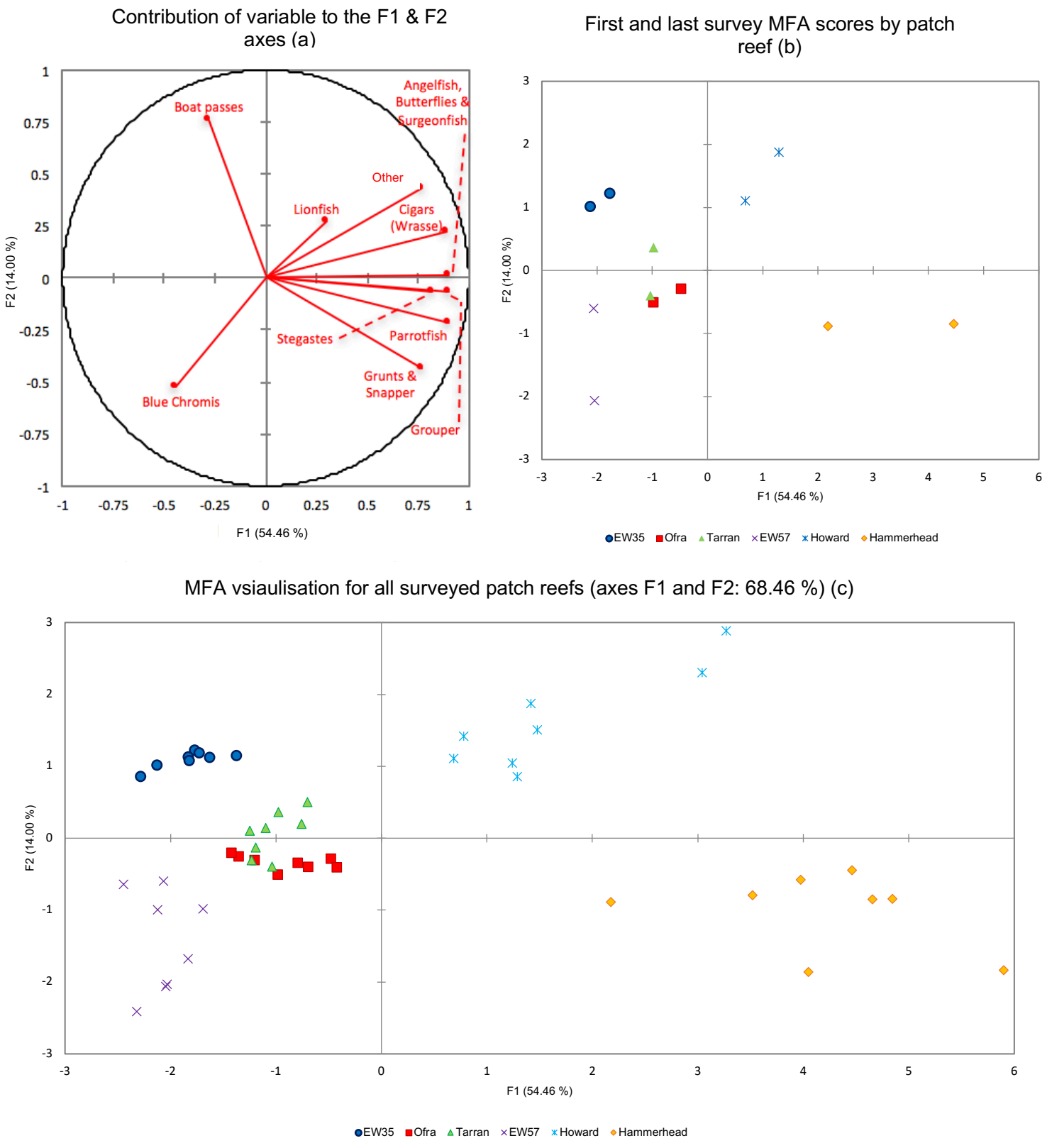

Figure 3.5. Multi Factor Analysis results for the effect of chronic noise on fish populations, exclusive of abiotic variables. (a) Contribution of each of the variables to the F1 and F2 axes. (b) MFA results from the first and last survey of each reef. (c) Full MFA results for all surveys on all patch reefs. Eigenvectors and factor loadings can be found in table 5.7.

reef's increase was substantial (Howard F1 = 0.390; Hammerhead F1 = 1.995).

The MFA was recreated without the abiotic factors to identify any trends in results based on the effect of population variables and boat traffic alone. The overall variation for F1 & F2 axes combined was slightly higher at 68.46% (*Figure 3.5*). The primary F1 factor loadings (54.46%) were the species inhabiting the reefs. The F2 factor loadings (14.00%) differed, with the primary contributor being the number of boat passes. With boat passes having a strong positive affect on the F2 axes, all trafficked sites understandably had higher F2 values than their protected partner reefs. All "avoid" reefs had negative F2 values. All but 3 surveys on the "traffic" reefs, all of which were on Tarran, had positive values. The larger reefs once again were the only reefs that had positive F1 values but had a much larger spread of results than the smaller reefs. The two smallest reefs both showed a decrease in F1 value over time (EW35 F1 = -0.359; Ofra F1 = -0.502), while the other pair of small reefs showed very little variation from start to finish but did still follow the same trend of the traffic reef decreasing and the avoid reefs increasing in F1 value (Tarran F1 = -0.059; EW57 F1 = 0.02). There was still a slight increase for F1 values of both of the larger reefs, but a palpable difference in the size of change with the protected reef benefitting from a superior increase (Howard F1 = 0.602; Hammerhead F1 = 3.857).

Notable results can be found when looking at the species richness and density of the surveyed species on each reef (*Figure 5.8 - Figure 5.12*). An advantageous part of this was comparing all the reefs based on the species richness per metre squared and the density as this provided an insight to the communities irrelevant to the total size of each reef. Where the MFA shows how all of the variables interact, this provides an insight into specific details. All 3 of the undisturbed patch reefs had higher densities than the reef partnered to them, with 2 of the 3 reefs having a noticeably increased density since the first survey. The reefs being treated with boat traffic also displayed increases in density, but it was minimal in comparison. There was little variation in species richness between reefs apart from EW57. Species richness was

initially well below its partner reef (Tarran = 17 species; EW57 = 11 species), but by the end of the study the two reefs showed very similar community sizes (Tarran = 15 species; EW57 = 14 species). The transformation of EW57 over the short period of time was so vast that by the end, the results showed no significant difference from those of Tarran which had far larger and varied community at the start of the study (density ANOVA: $F_{2.4/1079.7}$= 0.03, P > 0.05; species richness ANOVA: $F_{9/60}$= 1.48, P > 0.05). EW35 and Ofra showed very little difference throughout the study in species richness (EW35 mean = 15.125 species; Ofra mean = 14.125 species). EW35 maintained a density with only slight fluctuations where as Ofra had quite varied results with a gradual decrease overall (EW35 mean = 9.99; Ofra mean = 12.49). ANOVA testing showed there was a significant difference between these populations for density (ANOVA: $F_{25.1/57.6}$= 6.09, P < 0.05) but not for species richness (ANOVA: $F_{4/37.5}$= 1.48, P > 0.05). The largest two reefs maintained similar species richness per square metre throughout (Howard mean = 0.525; Hammerhead mean =0.523) but overall the “avoid” reef had a larger total species richness (Howard = 25.25; Hammerhead mean = 28). Density was a very different result, with the protected reef having a larger mean across all of the surveys conducted (Howard mean =3.81; Hammerhead mean =25.49) and recording a maximum result more than 10 times that of its comparative partner’s maximum surveyed population (Howard = 4.33; Hammerhead = 51.65). The disparity was substantially reduced when the population of juvenile *Haemulidae spp.* was not included in calculation (Howard mean = 2.93; Hammerhead mean = 3.76). These two reefs were shown to be significantly different when their populations were tested for density using an ANOVA test both with and without the inclusion of the *Haemulidae* population (total density ANOVA: $F_{877.6/1878.5}$= 29.97, P < 0.01; ANOVA: density without *Haemulidae spp.* $F_{2.77/5.72}$= 6.79, P < 0.05).

A slight anomaly that appears in the data set for every reef is a peak in abundance around the fourth, fifth and sixth surveys. There additionally seems to be a general trend in increasing populations throughout. As all of the reefs experienced this it would suggest that there is a natural increase in population around this time, and this needs to be considered when

reviewing results. This may be due to seasonal variation as the survey was conducted from spring through to summer (March – June). This does not appear to have an overt effect on the data set for most of the reefs, with the exception of patch reef Howard, where the fourth and fifth surveys have much larger F1 values compared with other surveys.

3.4 Discussion

There is a visible relationship between boat traffic and the patch reef populations of this study. The difficulty is determining exactly what is happening in detail and why the larger reefs appear to be affected differently to smaller ones. As information from statistical analysis is combined, the results provide information on how the communities in this study were affected by chronic exposure to anthropogenic noise.

Reefs that have previous exposure to boat traffic showed minimal change with an increase in boat traffic. They continued to have a lower abundance and density than similar reefs that had limited noise pollution prior to the study, and maintained similar, but varied, species richness. The lack of difference between the two reefs, EW35 & Ofra, is either because of the negative effects of previous exposure or may be related to the activity of local fishermen removing fish from the reefs, therefore influencing the outcome. The fishermen also added unrecorded boat traffic exposure that could not be controlled. Ofra, the protected reef, actually had recorded exposure levels closer to that of a “traffic” reef than the other “avoid” reefs (*Table 3.2*), which will have only increased with the passing fisherman. When looking at the MFA that compares only the species and boat traffic exposure (*Figure 3.5.*), again Ofra overlaps with Tarran and looks similar to other traffic reefs than with the avoid reefs. It must also be considered that Ofra and EW35 were exposed to high levels of boat traffic for a long period of time prior to the study. The other study sites all showed an increase in density over time, whereas both of these reefs did not. In fact, the decline in total population was up to 26%. This overall effect could be summed up by the lack of recruitment of juvenile *Haemulidae spp.* at these reefs

both before and during this study, whereas all the other reefs had larger starting populations and showed an increase over time. This could mean that once a minimum threshold of exposure is passed, which in this case may not even be daily exposure, it may start to affect the population of affected reefs as well as the reef's ability to recruit. Further to this, long-term exposure will take communities an extended period more than the time, longer than that covered in this study, to recover.

An observable result that strongly demonstrated the negative affect of anthropogenic noise from boats on fish communities came from the results of the other pair of small reefs that had limited exposure to boat traffic prior to the study, EW57 and Tarran. The reef being avoided by boat traffic, EW57, showed a substantial increase in species richness, while the opposite was true for the reef that experienced an increase in boat traffic, Tarran. The reef with increased frequency of anthropogenic noise also showed a relatively slower increase in density when equated to the protected site. It appears that the quiet patch reef is offering an attractive settlement option to an increasing number of species and is the community of a growing number of individuals. One family that showed a substantial increase in population was *Haemulidae spp.*; numbers only doubled on the traffic reef that had a larger population at the beginning of the study, whereas the un-trafficked reef experienced a population increase of 20 times compared with the population at the beginning of the study and double that of Tarran. This shows the vulnerability of the long-term health to reef recruitment to boat traffic, and perhaps highlights the sensitivity that fish have when using auditory cues to settle. This negative selection for certain noises is known to occur amongst settling fish as well as positive selection based on healthy reef sound (Simpson et al. 2004; Simpson et al., 2011). This is an area that requires continued research to better understand the use of auditory cues by both adults and juveniles, as well as how they are influenced by anthropogenic noise.

The largest pair of patch reefs were both able to grow in density and species richness, irrelevant of treatment. However, the trafficked reef was unable to maintain its population.

Even with a sudden drop in population of the untreated reef on the final survey, it still maintained an increase in the difference between itself and the other reef across species richness and density. Again, this shows that there is a clear negative affect on a reef experiencing high levels of boat traffic. The large juvenile *Haemulidae spp.* population, ever present at the protected reef, was thought to perhaps have an influence on the results, but this was not the case when the results were checked discounting *Haemulidae spp.* The trafficked reef showed lower abundance and species richness compared to that of its counterpart. The juvenile *Haemulidae spp.* led to the identification of another important outcome. Like the previous set of reefs, the reef which was exposed to an increase in boat traffic had a lower rate of recruitment than its counterpart. The population on reef Howard increased by less than double compared with over two and a half times the starting population in a traffic protected area. The difference here is that, a larger reef may still manage to recruit, even with an increase in boat traffic, but this will be beneath the threshold of other similar reefs that are protected from boat traffic.

A notable feature of all the data sets is the increased variation in the results for all the quiet reefs compared to their trafficked counterparts. This entails that more species are visiting these reefs. This ties in with what the rest of the analysis suggests, and previous studies. Even if there is no immediate detrimental effect to the population, recruitment of both adults and juveniles may be compromised for reefs in high traffic areas (Holles et al., 2013; Simpson et al. 2008). This is particularly prominent with the recruitment of juvenile *Haemulidae spp.* seen in the results of this study. Limited changes such as a different species of seagrass is known to cause change in *Haemulidae spp.* population. It is not surprising that changing the soundscape around patch reefs will affect recruitment given this.

3.4.1 Limitations

The lack of replication of results in this study limits the reliability of the outcome. During the planning of the study, compromise had to be made between budget, time and resources. Due

to the restrictions in place, it was chosen to focus on a variety of communities so a picture could be created of how the effects of anthropogenic noise may vary across changing habitats, which has been achieved. This did, however, mean that there were no replicates for each data set to compare, although there were some overlaps in size and previous exposure that have been discussed. Another concern was appearances of unusual species. For example, at one of the smaller reefs a nurse shark was lying on the bottom under the reef upon the first survey, but was not present thereafter. These data were included as species that roamed large areas appeared on many other reefs more regularly were included, but this was likely an anomaly that displaced results.

The actions of fishermen were an influence that could not have been avoided. On reef Ofra, located in an area commonly visited by fishermen, there were initially three Nassau grouper, but the population was steadily reduced. It could not be proved that the local fishermen were responsible for this, so the data were not changed to ignore this. Leading on from this, the inability to fully control boat traffic was another limitation and will be for almost any study of this nature. The boat traffic in the area almost exclusively consisted of the small local fishing boats and the vessels of the research station. Even with buoys as a visual cue and electronic marking using the GPS on the boats from the research station, some incursions of the 250 m exclusion zone around avoid reefs still occurred. All of the passes by vessels from the research station were noted but not those from the local fishermen (*Table 3.2*). This will have had the most notable effect on the two smallest reefs, EW35 and Ofra and could partially explain why the results for this pair seem to follow a slightly different trend to the other pairs. Due to the smaller draft of the fishermen's vessels, they were able to travel closer to the coast than the research vessels, which virtually all went out via EW35 when working in the patch reef system. This meant that they would avoid disturbing EW35 (traffic), but would regularly pass Ofra (avoid).

There was limited consideration given to meteorological and temporal changes outside of conducting surveys at similar times. The negative impact of this on the results of this study is minimal however, as all the patch reefs will have been affected equally, as seen with the apparent seasonal peak in population for the reefs. Regularity of boat noise is an issue as this varies even within the small area used in this study. As you increase variation in oceanography, types of vessels and weight of traffic, the effects could vary further. This is a demonstration of how varied communities reacted to a certain type and weight of traffic, but is not going to be an exact reflection or model for every system. Although it did not directly diminish the study, abstract data consisting of acoustic recordings of the craft in the area would have provided a small additional detail to enhance understanding of the vessels travelling the area for future reference. Additionally, a short study monitoring all vessels traversing the area would provide valuable data that would enhance interpretation of results.

The regularity of boat traffic was a potential issue. As the area has been so infrequently travelled in the past, the increase in boat traffic provided by this study will have had an effect, but may not have been enough to effect results in heavier trafficked areas. An alternative option would be to play recordings at regular intervals, but this negates the physical effect of a boat passing.

3.4.2 Future study

This study has yielded results with some key limitations being identified, but the real outcome is the development of the methodology that can now be replicated with improved accuracy and reliability. The key limitation to this study, and primary opportunity for further study, is the lack of replicates for each type of reef. Adding extra reefs with similar physical characteristics, populations, locations and previous exposure to boat noise would give results with increased reliability. If this could be achieved it would provide a more accurate description of the chronic effects of boat traffic on coral reef fish populations. This would best be achieved with an in depth pre-emptive study of potential sites, including variations in seasonal populations. If all

this could be accomplished, a long-term study could be developed over a large area to look at wider consequences. It could be achieved in other areas where there are not distinct patch reefs by using buoys to mark a boat channel and completing transect surveys.

Additional supporting data were another limitation here that could be capitalized on in future, with a particular focus turning to the collection of data on anthropogenic noise. There have been other studies that have used hydrophones to monitor boat traffic as well as biological sound (Veirs et al. 2016; Merchant et al.; 2012; Merchant et al., 2016; Freeman et al., 2014). Reef exposure could be recorded with increasing accuracy, while detailed abstract data could be collected about vessels in the area and the affect they are a having. Using hydrophones in place at the study site, or sites, would additionally enable the identification of passing boat traffic from other sources, such as the fisherman in this study. Simultaneously, the sound output from reefs in the area could be monitored for changes over time and acute reactions to passing traffic.

A specific fall out from this study was the effect that anthropogenic noise was having on juvenile *Haemulidae spp.* recruitment to patch reefs. This is something that should be studied further on surrounding reefs as well as at other locations in the Caribbean to determine if the same affect is present or whether it is unique to the Cape of Eleuthera. To determine if other species recruitment is affected in the same way would be interesting to see. If other species are identified as having a similar reaction, this would provide further routes for investigation.

The best opportunity for a study such as this, however, would be over a large area where channels could be created. Each channel would have its own characteristic; larger vessels, smaller vessels with a speed limit, smaller vessels unrestricted and no traffic. This would enable a study to identify whether controls over vessels speed and size had any effect and would provide excellent guidelines for boat traffic within MPAs.

3.4.3 Summary

Setting out to ascertain the effect of boat traffic on patch reef communities, this study has identified several key findings that should influence both future study and the way in which marine life is protected from anthropogenic noise. Concerningly, this study found that communities suffering from long term exposure to regular boat traffic showed no sign of growth despite being protected. This data demonstrates the requirement for protection and the long life plans that would need to be enacted to successfully undermine the negative effects of noise from boat traffic on patch reef communities. On the other hand, the data collected has highlighted positive effect of protection on communities that have less regular traffic. Protected reefs showed an increase in both species richness and density. Protection also offers the bonus of encouraging settlement of intermediate nursery species, in this case the large schools of *Haemulidae spp.* making the move from mangroves and seagrasses to larger reefs. The importance of these findings is clear. The longer the anthropogenic noise is exposed to a community, the harder it becomes to reverse the negative impact it has. Early protection will not only boost coral reef communities, but encourage further settlement. This study has only touched the cusp of these impacts and offers an opportunity for expansion into more detailed work. Achieving this could provide an insight into how manipulation of boat traffic could help protect populations of marine species whilst still allowing access for local communities.

4. Conclusion

This is the first study to look at the relationship between *Stegastes spp.* and *Haemulidae spp.* in the Cape of Eleuthera, whilst also being the first to attempt to explore the effect of anthropogenic noise on coral reef communities as a whole, rather than focusing on a limited number of species. The data and analysis recorded in these studies enables a broader understanding of how unusual relationships may shape the communities within an expansive series of patch reefs, as well as the ways in which the noise from vessels navigating the area may impact this vital nursery ground.

The outcome of the two data chapters produces an intriguing overlap in the recruitment of *Haemulidae spp*. Chapter 2 exhibited the influence that *S. diencaeus* and *S. leucostictus* had on settlement of *Haemulidae spp.* passing through the patch reefs system. As the *Haemulidae spp.* intermediates progressed from the seagrass and mangroves towards the fore reefs, they were locating themselves in large schools around the two Stegastes spp., whilst appearing to settle in much lower numbers where S. partitus was present. Similarly, chapter 3 demonstrated that patch reefs protected from regular boat traffic developed notably larger populations of *Haemulidae spp.* than those that were not. Additionally, the protected reefs generally had healthier communities with a greater species richness and a higher density than those that were not protected. This potentially produces an exciting opportunity to simply monitor reef health and protect the nursery with simple surveys. The presence of the large *Haemulidae spp.* schools were on the healthy reefs, which will continue to recruit if protected. These schools were also linked to reefs populated by *S. diencaeus*, which was identified as topping the *Stegastes spp.* hierarchy to dominate the optimal reefs. Therefore, identifying reefs with large schools of Haemulidae spp., *S. diencaeus*, or both, offers a simple strategy to implement protection of both the healthiest reefs and those key to the success of the nursery. As it is likely that this nursery system feeds a large number of reefs, the importance of which was identified in the literature review, protection from boat traffic based on these findings could

have an immensely positive effect on the output of the nursery system by increasing the number of suitable reefs for settlement for *Haemulidae spp*. With careful planning, this concept could still allow for access channels for both tourist vessels and local fisherman, enabling an MPA that benefits both its marine species and the surrounding local communities. Pushing this concept to nurseries across a wider scale, or adding it to MPAs already in place, could uplift the input of nurseries in providing adult populations on fore reefs. This said, should the findings be ignored, the negative effects of long term exposure, as seen in this study, may slowly diminish the positive benefit of this nursery system.

It is clear, however, that *Stegastes spp.* have also played a key part in the settlement of *Haemulidae spp.*, and therefore in influencing reef health. Monitoring the genus offers great potential for supporting the nursery and developing any plans for protection, making the detail deciphered by this study on the niches *Stegastes spp.* occupy key. Settling in reefs with regular small holes in the substrata was the common theme across all the species surveyed that could identify why *Stegastes spp.* are not settling on certain reefs as well as enable the design and production of artificial reefs in areas where the populations may be struggling. Understanding how the physical structure suits *Stegastes spp.* and supporting the habitat that suits them, and likely other small fish species, may in turn support the settlement of *Haemulidae spp.* The clear hierarchy amongst the species once again links into the key relationship with *Haemulidae spp.* and reef health. The presence of *S. partitus,* relegated away from the optimal reefs by *S. diencaeus,* did not correlate with the presence of schools of *Haemulidae spp.* Future studies should consider if *S. Partitus* is perhaps as sign of less healthy coral reef communities, as well as the opposite for *S. diencaeus*.

Looking forwards beyond these findings, the relationship between the *Haemulidae spp.* and *Stegastes spp.* could shed further detail on reef health and the detrimental effects of anthropogenic noise. The understanding developed from this study should form the basis of wider and more detailed studies of a similar nature, both in the waters of the Cape of Eleuthera

and in other nurseries. Future studies should seek to focus on how these species relate to the wider communities of nursery habitats, whilst continuing to look at the community wide effects of anthropogenic noise. This will further understanding of the factors underpinning reef health, enhancing protection of coral patch reef nurseries and the communities they support.

5. Appendices

5.1 Appendix to Chapter 2 – Interactions in habitat occupation by *Stegastes spp.* and *Haemulidae spp.* at Cape Eleuthera in The Bahamas

Table 5.1 Original data for Stegastes spp. settlement MFA. Individuals highlighted in light grey were not included in analysis as detailed in chapter 2.

Species	Reef name	Depth / cm	Widest width / cm	Wides perpendicular width / cm	Height of patch reef / cm	Height *Stegastes spp.* from sea bed / cm	Number of holes in *Stegastes spp.* territory	Average diameter of hole in *Stegastes spp.* territory / mm	Number of *Haemulidae spp.* surrounding *Stegastes spp.* territory	Total number of *Haemulidae spp.* surrounding patch reef
S. partitus	Esther	268	173	172	109	109	9	8.22	0	0
S. partitus	Esther	268	106	84	119	119	8	8.75	0	0
S. partitus	Esther	268	187	174	77	77	4	15.50	0	0
S. partitus	Esther	268	187	174	47	47	6	6.67	0	0
S. partitus	Esther	268	109	67	77	77	9	5.78	0	0
S. partitus	Esther	268	299/56	276/50	150/86	86	1	4.00	0	0
S. diencaeus	Harrin	275	256	248	186	156	5	12.60	550	2800
S. diencaeus	Harrin	275	256	248	186	90	1	19.00	550	2800
S. diencaeus	Harrin	275	534	276	126	126	4	15.50	500	2800
S. diencaeus	Harrin	275	534	276	126	91	5	10.80	500	2800
S. leucostictus	Harrin Mk2	275	203	137	75	27	2	12.00	0	0
S. leucostictus	Harrin Mk2	275	203	137	75	57	5	10.60	0	0
S. leucostictus	Harrin Mk2	275	76	32	21	15	3	5.33	0	0
S. leucostictus	Harrin Mk2	275	76	65	20	15	1	25.00	0	0
S. leucostictus	Harrin	275	-	-	121	87	7	11.57	50	2800
S. leucostictus	Harrin	275	-	-	121	67	0	0	50	2800
S. partitus	57	360	292	217	118	75	3	15.67	10	150
S. partitus	57	360	142	108	68	71	1	18.00	0	150
S. leucostictus	FWA	370	106	99	68	0	9	18.22	500	2200
S. leucostictus	FWA	370	103	58	58	28	5	20.20	500	2200
S. diencaeus	FWA	370	111	36	101	20	2	27.00	300	2200
S. diencaeus	FWA	370	180	150	102	79	10	21.00	300	2200
S. adustus	FWA	370	110	83	82	56	3	16.33	500	2200
S. adustus	FWA	370	90	87	90	60	10	-	0	2200
S. partitus	Tiny	331	265	207	119	109	10	13.30	50	1500
S. partitus	Tiny	331	215	123	121	121	2	11.00	200	1500
S. partitus	Tiny	331	84	70	59	33	4	9.50	20	1500
S. leucostictus	C4	282	244	142	110	80	4	17.75	20	3000
S. partitus	C4	282	244	142	110	19	3	12.00	20	3000
S. leucostictus	C4	282	253	137	140	90	10	13.00	0	3000
S. leucostictus	C4	282	220	126	50	15	1	19.00	0	3000
S. leucostictus	C4	282	151	128	76	19	0	13.00	0	3000
S. leucostictus	C4	282	134	105	80	14	2	0	60	3000
S. leucostictus	C4	282	120	77	66	44	1	15.50	0	3000
S. diencaeus	C4	282	25	25	60	50	0	15.00	0	3000

Table 5.2 One-way ANOVA results for Stegastes spp. settlement variables.

Analysis of Variance (One-Way) - Number of *Haemulidae spp.* around patch reef

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	28000.00	2000.00	1796923.08
S. partitus	12.00	7800.00	650.00	975000.00
S. diencaeus	7.00	18600.00	2657.14	102857.14

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	20815281.39	2.00	10407640.69	9.00	0.00	4.47
Within Groups	34702142.86	30.00	1156738.10			
Total	55517424.24	32.00				

Analysis of Variance (One-Way) - Number of *Haemulidae spp.* around *Stegastes spp.* territory

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
Beaugregory	14.00	1180.00	84.29	31503.30
Bicolour	12.00	300.00	25.00	3263.64
Longfin	7.00	2700.00	385.71	40595.24

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	618919.05	2.00	309459.52	13.47	0.00	4.47
Within Groups	689014.29	30.00	22967.14			
Total	1307933.33	32.00				

Table 5.2 (continued) One-way ANOVA results for Stegastes spp. settlement variables.

Analysis of Variance (One-Way) - Widest perpendicular width

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	12.00	3132.00	130.50	3403.91
S. partitus	12.00	3648.00	152.00	4611.74
S. diencaeus	7.00	3155.00	225.36	25808.40

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	82220.16	2.00	41110.08	4.67	0.01	4.18
Within Groups	519869.21	28.00	8811.34			
Total	602089.37	30.00				

Analysis of Variance (One-Way) - Height of *Stegastes spp.* from sea floor

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	558.00	39.86	942.13
S. partitus	12.00	943.00	78.58	1094.45
S. diencaeus	7.00	612.00	87.43	2037.95

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	14554.62	2.00	7277.31	5.98	0.01	4.47
Within Groups	36514.35	30.00	1217.14			
Total	51068.97	32.00				

Table 5.2 (continued) One-way ANOVA results for Stegastes spp. settlement variables.

Analysis of Variance (One-Way) - Height of *Stegastes spp.* relative to reef height

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	710.16	50.73	618.46
S. partitus	12.00	1032.77	86.06	715.76
S. diencaeus	7.00	485.07	69.30	719.02

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	8097.57	2.00	4048.79	6.00	0.01	4.47
Within Groups	20227.41	30.00	674.25			
Total	28324.98	32.00				

Analysis of Variance (One-Way) - Height of reef

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	1081.00	77.21	1278.80
S. partitus	12.00	1110.00	92.50	705.55
S. diencaeus	7.00	887.00	126.71	2125.57

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	11445.76	2.00	5722.88	4.62	0.02	4.47
Within Groups	37138.79	30.00	1237.96			
Total	48584.55	32.00				

Table 5.2 (continued) One-way ANOVA results for Stegastes spp. settlement variables.

Analysis of Variance (One-Way) - Widest width						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
S. leucostictus	12.00	1889.00	157.42	4141.54		
S. partitus	12.00	2060.00	171.67	5541.52		
S. diencaeus	7.00	1896.00	270.86	38864.14		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	62473.24	2.00	31236.62	2.57	0.09	4.51
Within Groups	339698.44	28.00	12132.09			
Total	402171.68	30.00				

Analysis of Variance (One-Way) - Number of holes within *Stegastes spp.* territory						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
S. leucostictus	14.00	50.00	3.57	10.57		
S. partitus	12.00	60.00	5.00	10.73		
S. diencaeus	7.00	27.00	3.86	11.14		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	13.96	2.00	6.98	0.65	0.53	4.47
Within Groups	322.29	30.00	10.74			
Total	336.24	32.00				

Table 5.2 (continued) One-way ANOVA results for Stegastes spp. settlement variables.

Analysis of Variance (One-Way) - Mean hole size within *Stegastes spp.* territory

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	119.63	8.54	19.51
S. partitus	12.00	111.81	9.32	15.19
S. diencaeus	7.00	54.80	7.83	19.46

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	10.20	2.00	5.10	0.28	0.75	4.47
Within Groups	537.40	30.00	17.91			
Total	547.60	32.00				

Analysis of Variance (One-Way) - Depth

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
S. leucostictus	14.00	4082.00	291.57	1115.34
S. partitus	12.00	3603.00	300.25	1504.57
S. diencaeus	7.00	2122.00	303.14	2092.48

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	802.37	2.00	401.19	0.28	0.76	3.32
Within Groups	43604.54	30.00	1453.48			
Total	44406.91	32.00				

Table 5.3 Eigenvectors & Factor Loadings for Stegastes spp. settlement MFA. Note that the variable of Stegastes spp. height relative to the reef is not included as a variable for the MFA as the test would consider this relationship in its statistics. The major contributors to both F1 and F2 had values >0.3 for eigenvectors and >0.5 for factor loadings. The factor loadings are the scores that are plotted on the graphs for the MFA.

	Eigenvectors		Factor Loadings	
Variable	F1	F2	F1	F2
Depth	-0.054	0.497	-0.101	0.688
Widest width of *Stegastes* territory	0.451	-0.036	0.840	-0.050
Width perpendicular to that of the largest width of *Stegastes* territory	0.477	-0.098	0.890	-0.136
Height of patch reef from sea bed	0.472	0.021	0.881	0.029
Height of the *Stegastes spp.* from sea bed	0.413	-0.228	0.771	-0.316
Number of holes in *Stegastes* territory substrata	0.162	-0.208	0.303	-0.288
Average diameter of hole in the *Stegastes.* territory substrata	0.004	0.579	0.007	0.803
Number of *Haemulidae spp.* surrounding a *Stegastes spp.* territory	0.333	0.402	0.622	0.557
Total number of *Haemulidae spp.* surrounding the patch reef	0.186	0.388	0.347	0.538

5.2 Appendix to Chapter 3 - Impacts of chronic boat traffic on coral reef populations in The Bahamas.

Table 5.4 Species surveyed on experimental reefs. Each species is sorted into a group for use in MFA.

Serial	Lionfish	Blue Chromis	Damselfish	Wrasse	Angelfish, Butterflyfish and Surgeonfish	Grouper	Grunt & Snapper	Parrotfish	Other
1	Lionfish	Blue Chromis	Bicolour	Blue Headed Wrasse	Rock Beauty	Nassau	Mutton Snapper	Stoplight Parrotfish	Sharpnose puffer
2			Longfin	Yellow Headed Wrasse	Blue Tang	Black Grouper	White Margate	Striped Parrotfish	Squirrelfish
3			Cocoa	Slippery Dick	Queen Angelfish	Graysby	White Grunt	Red Band Parrotfish	Queen Triggerfish
4			Beaugregory	Pudding Wife	Grey Angelfish	Rock hind	French Grunt	Green blotch Parrotfish	Cardinalfish
5			Dusky		Doctorfish		Blue Stripped Grunt	Redtail Parrotfish	Reef Squirrelfish
6					Foureye Butterflyfish		Yellowtail Snapper		Sharpnose puffer
7					Ocean Surgeonfish				Porgy
8					Rock Beauty				Yellow Ray
9									Hogfish
10									Fairy Basslet
11									Porcupine fish
12									Nurse Shark
13									Sharksucker
14									Ocean Triggerfish
15									Barracuda
16									Alcamo Jack
17									Barracuda
18									Bar jack
19									Cero
Total species	53								

Table 5.5 Data for impact of chronic boat noise MFA. The data collected from each survey (1-8) of each experimental reef.

Reef	Replicate	Boat passes	Depth / m	Widest width / m	Perpendicular width / m	Average Chain / mm	Lionfish	Blue Chromis	Damselfish	Wrasse	Angelfish, Butterflyfish and Surgeonfish	Grouper	Grunt & Snapper	Parrotfish	Other
EW35.1	1	55	2.85	2.8	1.9	74	0	2	1	24	8	2	0	8	3
EW35.2	2	55	2.85	2.8	1.9	74	0	3	1	18	7	0	1	18	1
EW35.3	3	55	2.85	2.8	1.9	74	0	2	5	23	8	0	0	15	2
EW35.4	4	55	2.85	2.8	1.9	74	0	2	4	17	10	1	1	19	4
EW35.5	5	55	2.85	2.8	1.9	74	0	2	4	16	8	1	2	16	3
EW35.6	6	55	2.85	2.8	1.9	74	0	2	4	26	9	2	1	18	3
EW35.7	7	55	2.85	2.8	1.9	74	0	2	3	23	9	1	0	13	3
EW35.8	8	55	2.85	2.37	2.12	74	0	2	3	9	6	1	5	15	3
Ofra.1	1	16	1.9	2.37	2.12	87	0	1	16	23	3	3	7	21	3
Ofra.2	2	16	1.9	2.37	2.12	87	0	1	11	18	3	1	0	23	2
Ofra.3	3	16	1.9	2.37	2.12	87	0	1	10	21	3	1	0	15	1
Ofra.4	4	16	1.9	2.37	2.12	87	0	1	7	15	9	1	0	10	2
Ofra.5	5	16	1.9	2.37	2.12	87	0	2	15	32	6	2	0	26	2
Ofra.6	6	16	1.9	2.37	2.12	87	0	2	11	20	7	3	0	14	4
Ofra.7	7	16	1.9	2.37	2.12	87	0	2	15	21	8	2	0	15	3
Ofra.8	8	16	1.9	3.3	2.45	87	0	2	15	15	6	2	2	13	2
Tarran.1	1	19	3	3.3	2.45	73.58571429	1	0	11	21	5	1	48	9	4
Tarran.2	2	19	3	3.3	2.45	73.58571429	2	0	11	29	4	0	25	27	3
Tarran.3	3	19	3	3.3	2.45	73.58571429	1	0	11	15	3	0	22	31	3
Tarran.4	4	19	3	3.3	2.45	73.58571429	1	2	10	17	4	0	24	30	4
Tarran.5	5	19	3	3.3	2.45	73.58571429	2	1	12	27	3	0	21	34	2
Tarran.6	6	19	3	3.3	2.45	73.58571429	1	2	13	15	2	1	22	23	1
Tarran.7	7	19	3	3.3	2.45	73.58571429	1	0	9	10	6	1	64	17	2
Tarran.8	8	19	3	3.2	2.3	73.58571429	0	1	9	13	6	1	103	38	2

Table 5.5 (continued) Data for impact of chronic boat noise MFA. The data collected from each survey (1-8) of each experimental reef.

Reef	Replicate	Boat passes	Depth / m	Widest width / m	Perpendicular width / m	Average Chain / mm	Lionfish	Blue Chromis	Damselfish	Wrasse	Angelfish, Butterflyfish and Surgeonfish	Grouper	Grunt & Snapper	Parrotfish	Other
EW57.1	1	2	2.9	3.2	2.3	79.851	0	0	3	12	3	0	10	8	0
EW57.2	2	2	2.9	3.2	2.3	79.851	0	0	0	5	2	0	10	7	0
EW57.3	3	2	2.9	3.2	2.3	79.851	1	3	2	6	3	0	11	20	2
EW57.4	4	2	2.9	3.2	2.3	79.851	2	4	3	20	2	1	12	21	0
EW57.5	5	2	2.9	3.2	2.3	79.851	3	8	8	11	3	0	13	28	0
EW57.6	6	2	2.9	3.2	2.3	79.851	0	8	3	18	3	1	18	27	2
EW57.7	7	2	2.9	3.2	2.3	79.851	2	11	3	13	2	1	158	19	0
EW57.8	8	2	2.9	7.63	6.3	79.851	2	9	2	16	3	1	212	21	0
Howard.1	1	28	2.6	7.63	6.3	79.33333333	4	0	11	27	17	4	48	30	4
Howard.2	2	28	2.6	7.63	6.3	79.33333333	2	0	15	53	15	3	39	11	19
Howard.3	3	28	2.6	7.63	6.3	79.33333333	3	0	13	41	20	1	75	52	15
Howard.4	4	28	2.6	7.63	6.3	79.33333333	5	0	12	51	15	6	8	53	35
Howard.5	5	28	2.6	7.63	6.3	79.33333333	3	0	16	77	13	4	17	54	25
Howard.6	6	28	2.6	7.63	6.3	79.33333333	2	1	7	44	15	4	50	56	13
Howard.7	7	28	2.6	7.63	6.3	79.33333333	3	0	12	31	14	1	49	45	14
Howard.8	8	28	2.6	7.63	6.3	79.33333333	0	0	17	40	14	3	56	46	14
Hammerhead.1	1	6	2.9	10.5	5.1	71.98333333	1	0	10	34	28	4	916	58	6
Hammerhead.2	2	6	2.9	10.5	5.1	71.98333333	1	0	24	54	31	10	933	71	10
Hammerhead.3	3	6	2.9	10.5	5.1	71.98333333	1	0	17	62	31	6	915	70	10
Hammerhead.4	4	6	2.9	10.5	5.1	71.98333333	0	0	21	35	30	4	915	78	16
Hammerhead.5	5	6	2.9	10.5	5.1	71.98333333	0	0	20	72	27	6	857	109	11
Hammerhead.6	6	6	2.9	10.5	5.1	71.98333333	0	1	22	49	19	6	1424	106	8
Hammerhead.7	7	6	2.9	10.5	5.1	71.98333333	1	1	17	52	29	7	2525	110	21
Hammerhead.8	8	6	2.9	10.5	5.1	71.98333333	3	1	20	48	29	9	823	73	13

Table 5.6 Eigenvectors & Factor Loadings for the effect of chronic noise on fish populations, inclusive of abiotic variables. The major contributors to both F1 and F2 had values >0.3 for eigenvectors and >0.5 for factor loadings. The factor loadings are the scores that are plotted on the graphs for the MFA.

	Eigenvectors		Factor loadings	
Variable	F1	F2	F1	F2
Boat passes	-0.099	0.147	-0.263	0.209
Depth	0.070	0.653	0.186	0.927
Widest width	0.360	0.050	0.956	0.071
Perpendicular width	0.308	-0.103	0.818	-0.146
Rugosity (average chain length)	-0.152	-0.619	-0.402	-0.878
Lionfish	0.139	-0.055	0.369	-0.078
Blue chromis	-0.155	0.118	-0.411	0.168
Stegastes	0.286	-0.244	0.761	-0.347
Wrasse	0.332	-0.102	0.881	-0.145
Angelfish, Butterflies & Surgeonfish	0.345	0.048	0.915	0.067
Grouper	0.329	-0.085	0.873	-0.121
Grunts & Snapper	0.284	0.162	0.755	0.230
Parrotfish	0.341	0.084	0.906	0.120
Other	0.281	-0.161	0.745	-0.228

Table 5.7 Eigenvectors & Factor Loadings for the effect of chronic noise on fish populations, exclusive of abiotic variables. The major contributors to both F1 and F2 had values >0.3 for eigenvectors and >0.5 for factor loadings. The factor loadings are the scores that are plotted on the graphs for the MFA.

	Eigenvectors		Factor loadings	
Variable	F1	F2	F1	F2
Boat passes	-0.120	0.639	-0.279	0.756
Lionfish	0.129	0.232	0.302	0.275
Blue Chromis	-0.191	-0.442	-0.446	-0.523
Stegastes	0.350	-0.057	0.816	-0.068
Cigars (Wrasse)	0.380	0.185	0.887	0.219
Angelfish, Butterflies & Surgeonfish	0.388	0.013	0.906	0.016
Grouper	0.385	-0.059	0.898	-0.070
Grunts & Snapper	0.329	-0.367	0.768	-0.434
Parrotfish	0.388	-0.180	0.906	-0.213
Other	0.328	0.366	0.765	0.433

Table 5.8 Species richness recorded during each survey for each experimental reef.

Species richness	EW35	Ofra	Tarran	EW57	Howard	Hammerhead
1	14	15	17	11	24	25
2	13	11	17	9	24	26
3	14	14	15	16	25	29
4	16	16	16	16	26	27
5	16	15	15	14	24	26
6	17	12	15	15	24	25
7	14	15	14	17	28	35
8	17	15	15	14	27	31
Mean	15.125	14.125	15.5	14	25.25	28
Area	5.32	5.0244	8.085	7.36	48.069	53.55
Median	15	15	15	14.5	24.5	26.5
Mode	14	15	15	16	24	25
Standard deviation	1.553	1.727	1.069	2.726	1.581	3.505
Standard error	0.549	0.611	0.378	0.964	0.559	1.239

Table 5.9 Density of population recorded during each survey for each experimental reef.

Density	EW35	Ofra	Tarran	EW57	Howard	Hammerhead
1	9.023	15.325	12.369	4.891	3.037	19.739
2	9.211	11.743	12.492	3.261	3.266	21.158
3	10.338	10.349	10.637	8.016	4.577	20.710
4	10.902	8.956	11.503	8.967	3.911	20.486
5	9.774	16.917	12.616	10.054	4.327	20.598
6	12.218	12.141	9.647	10.734	3.994	30.532
7	10.150	13.136	13.605	28.533	3.516	51.653
8	8.271	11.345	21.521	36.141	3.890	19.010
Mean	9.986	12.489	13.049	13.825	3.815	25.486
Area	5.320	5.024	8.085	7.360	48.069	53.550
Median	9.962	11.942	12.430	9.511	3.901	20.654
Standard deviation	1.224	2.594	3.642	11.873	0.519	11.184
Standard error	0.433	0.917	1.288	4.198	0.183	3.954

Table 5.10 Density of population, not including Haemulidae spp., recorded during each survey for each experimental reef.

Density without *Haemulidae spp.*	EW35	Ofra	Tarran	EW57	Howard	Hammerhead
1	9.023	13.932	6.432	3.533	2.039	2.633
2	9.023	11.743	9.400	1.902	2.455	3.735
3	10.338	10.349	7.916	6.522	3.016	3.623
4	10.714	8.956	8.534	7.337	3.745	3.399
5	9.398	16.917	10.019	8.288	3.973	4.594
6	12.030	12.141	6.926	8.288	2.954	3.940
7	10.150	13.136	5.690	7.065	2.496	4.500
8	7.331	10.947	8.782	7.337	2.725	3.641
Mean	9.751	12.265	7.962	6.284	2.925	3.758
Area	5.320	5.024	8.085	7.360	48.069	53.550
Median	9.774	11.942	8.225	7.201	2.840	3.688
Standard deviation	1.397	2.444	1.506	2.320	0.656	0.622
Standard error	0.494	0.864	0.532	0.820	0.232	0.220

Table 5.11 Density of Haemulidae spp. recorded during each survey for each experimental reef.

Density of *Haemulidae spp.*	EW35	Ofra	Tarran	EW57	Howard	Hammerhead
1	0.000	1.393	5.937	1.359	0.999	17.106
2	0.188	0.000	3.092	1.359	0.811	17.423
3	0.000	0.000	2.721	1.495	1.560	17.087
4	0.188	0.000	2.968	1.630	0.166	17.087
5	0.376	0.000	2.597	1.766	0.354	16.004
6	0.188	0.000	2.721	2.446	1.040	26.592
7	0.000	0.000	7.916	21.467	1.019	47.152
8	0.940	0.398	12.740	28.804	1.165	15.369
Mean	0.235	0.224	5.087	7.541	0.889	21.727
Area	5.320	5.024	8.085	7.360	48.069	53.550
Median	0.188	0.000	3.030	1.698	1.009	17.096
Standard deviation	0.314	0.493	3.648	11.041	0.446	10.864
Standard error	0.070	0.088	0.239	0.415	0.083	0.412

Table 5.12 One-way ANOVA test results for species richness, density and density without Haemulidae spp. for each pair of patch reefs.

Analysis of Variance (One-Way) - Species richness (Hammerhead v Howard)						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
Hammerhead	8.00	224.00	28.00	12.29		
Howard	8.00	202.00	25.25	2.50		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	30.25	1.00	30.25	4.09	0.06	6.89
Within Groups	103.50	14.00	7.39			
Total	133.75	15.00				

Analysis of Variance (One-Way) - Species richness (Tarran vs EW57)						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
57.00	8.00	112.00	14.00	7.43		
Tarran	8.00	124.00	15.50	1.14		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	9.00	1.00	9.00	2.10	0.17	6.89
Within Groups	60.00	14.00	4.29			
Total	69.00	15.00				

Table 5.12 (continued) One-way ANOVA test results for species richness, density and density without Haemulidae spp. for each pair of patch reefs.

Analysis of Variance (One-Way) - Species richness (Ofra v EW35)						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
Ofra	8.00	113.00	14.13	2.98		
35.00	8.00	121.00	15.13	2.41		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*p-level*	*F crit*
Between Groups	4.00	1.00	4.00	1.48	0.24	6.89
Within Groups	37.75	14.00	2.70			
Total	41.75	15.00				

Analysis of Variance (One-Way) - Density (Hammerhead v Howard)						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
Hammerhead	8.00	203.88	25.49	125.08		
Howard	8.00	30.52	3.81	0.27		
ANOVA						
Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	1878.48	1878.48	29.97	0.00	4.60
Within Groups	14.00	877.46	62.68			
Total	15.00	2755.94				

Table 5.12 (continued) One-way ANOVA test results for species richness, density and density without Haemulidae spp. for each pair of patch reefs.

Analysis of Variance (One-Way) - Density (Tarran vs EW57)

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
EW57	8.00	110.60	13.82	140.98
Tarran	8.00	104.39	13.05	13.26

ANOVA

Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	2.41	2.41	0.03	0.86	4.60
Within Groups	14.00	1079.68	77.12			
Total	15.00	1082.09				

Analysis of Variance (One-Way) - Density (Ofra v EW35)

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
EW35	8.00	79.89	9.99	1.50
Ofra	8.00	99.91	12.49	6.73

ANOVA

Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	25.06	25.06	6.09	0.03	4.60
Within Groups	14.00	57.61	4.11			
Total	15.00	82.67				

Table 5.12 (continued) One-way ANOVA test results for species richness, density and density without Haemulidae spp. for each pair of patch reefs.

Analysis of Variance (One-Way) - Density without *Haemulidae spp.* (Hammerhead v Howard)

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
Hammerhead	8.00	30.07	3.76	0.39
Howard	8.00	23.40	2.93	0.43

ANOVA

Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	2.77	2.77	6.79	0.02	4.60
Within Groups	14.00	5.72	0.41			
Total	15.00	8.49				

Analysis of Variance (One-Way) - Density without *Haemulidae spp.* (Tarran vs EW57)

Summary

Groups	*Sample size*	*Sum*	*Mean*	*Variance*
EW57	8.00	50.27	6.28	5.38
Tarran	8.00	63.70	7.96	2.27

ANOVA

Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	11.27	11.27	2.94	0.11	4.60
Within Groups	14.00	53.56	3.83			
Total	15.00	64.83				

Table 5.12 (continued) One-way ANOVA test results for species richness, density and density without Haemulidae spp. for each pair of patch reefs.

Analysis of Variance (One-Way) - Density without *Haemulidae spp.* (Ofra v EW35)						
Summary						
Groups	*Sample size*	*Sum*	*Mean*	*Variance*		
EW35	8.00	78.01	9.75	1.95		
Ofra	8.00	98.12	12.27	5.98		
ANOVA						
Source of Variation	*d.f.*	*SS*	*MS*	*F*	*p-value*	*F crit*
Between Groups	1.00	25.28	25.28	6.38	0.02	4.60
Within Groups	14.00	55.50	3.96			
Total	15.00	80.78				

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